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A Monthly Journal
Devoted to the Advancement of the Biological Sciences
With Special Reference to the Factors of Evolution

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THE AMERICAN NATURALIST

A MONTHLY JOURNAL
DEVOTED TO THE NATURAL SCIENCES
IN THEIR WIDEST SENSE

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ERRATA

THE "Ichthyological Notes" in the December issue of THE AMERICAN NATURALIST (vol. 41) contain the following errata, since owing to unavoidable circumstances the number had to be issued before the author's proof was returned.

Page 788. For *Ch. mazquital* read *Ch. mezquital.*
For *Neomugil digneti* read *N. digueti.*
For Encinostomus read Eucinostomus.

Page 789. For *C. boveinus* read *C. bovinus.*
For *Zoogenaticus* read *Zoogoneticus.*
For Actinia read Adinia.
For *Ch. latevalis* read *Ch. lateralis.*
For *Charaeodon duitpoldi* read *Characodon luitpoldi.*
For *Ps. retiaulatus* read *Ps. reticulatus.*
For Heteraudria read Heterandria.
For *limantoun* read *limantouri.*
For *Mollienesia formora* read *M. formosa.*
For *Xiphophinus* read *Xiphophorus.*
For *Aelunchthys* read *Aelurichthys.*
For *Netuma vacula* read *N. oscula.*
For *Netuma clattena* read *N. elattura.*
For *G. Kessleri* read *G. kessleri.*
For Anus read Arius.
For *Tachysurus Steindachneri* read *T. steindachneri.*
For *Anus multeradiatus* read *Arius multiradiatus.*
For *Cathorops gulorus* read *C. gulosus.*

Page 790. For *Tetragonopterus humitis* read *T. humilis.*
For *Dorosome* read *Dorosoma.*

Page 791. For *Stercolepis* read *Stereolepis.*
For Mr. Alvin Seele read Mr. Alvin Seale.

Page 796. For Dr. J. Graham Kew read Dr. J. Graham Kerr.

Page 797. For *Isusus* read *Isurus.*

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EXPERIMENTS IN GRAFTING

PROFESSOR T. H. MORGAN

Columbia University

These experiments were undertaken primarily to find out whether it is possible by artificial means to induce regeneration in a part that does not regenerate under ordinary circumstances; and secondly to find out what kind of a structure will regenerate from the proximal end of so highly specialized an organ as the limb of a salamander; for, while we know that from the distal end a new limb regenerates we have no information as to what will happen if the proximal end is exposed. Since the latter experiments gave more positive results they will be first considered. As it is necessary to keep the limb alive during the relatively long period required for its regeneration it was necessary to graft it, in a reversed position, on to the same animal.

The following method of grafting was employed. The leg was cut off, the skin loosened around the attached stump and turned back. The stump (composed of muscles, bone, nerves, etc.) was cut off higher up and the skin was then turned back. A pocket was thus formed. Into this pocket the piece cut off was implanted, after being turned around so that its proximal end was directed outwards. The skin was then drawn together by a ligature over the cut end. Since it is desirable to draw the skin completely over the exposed end without, however, pressing too much on the grafted piece, I have found it desir-

able to cut off a longer piece of the stump than will be required, and then to cut this in half, putting either half back into the pocket, which being incompletely filled, allows the skin to be drawn more readily over the end. The hind-limb being larger was used. The implanted piece, reversed in orientation, consists of bones, muscles, nerves, etc. The skin covering these parts is the old skin with normal orientation. Therefore, at least one element in the complex is not reversed.

In some respects this method of grafting proved unsatisfactory, because the cut end of the stump is so near to the graft that the new material from the stump and that from the graft may easily become mixed, so that the results would be complicated. The shortness of the grafted piece is another source of difficulty, since the short piece may become displaced during the healing of the end. To overcome these difficulties I devised another method, in which however only a single organ has its orientation reversed. The hind leg was cut off at the knee, and the femur removed from the stump for nearly its entire length. It is then shortened by cutting off part of one end, and pushed back into its original position, but with its orientation reversed. Owing to the slightly bent shape of the femur, and its much enlarged knee-end, no chance for a mistake in its orientation is possible. This procedure proved superior to the first, although the problem involved is somewhat different.

At first the large salamander, *Spelerpes ruber,* was used. This is a terrestrial form. Later the somewhat smaller *Diemyctylus viridescens* was used. Both species withstand the operation well and regenerate readily. Serial sections were made of the limbs at different stages of their regeneration.

Regeneration from the Proximal End of a Reversed Piece

An examination of the preparations of those cases in which a cross-section of the limb was implanted in a

reverse direction in the pocket of skin of the same limb shows that as a rule proliferation takes place from the cut ends of the bones, both of the graft and of the stump of the limb. In the majority of cases it is impossible to decide with certainty whether the bones of the new limb originate from one or from both sources. While such a combined formation would be of interest in itself the conditions are such as to make it impossible to assert that both proliferations do actually contribute; for, even if the new material from both sources is continuous with the new material of the regenerating part, we can not be entirely certain that both really take part, however probable this may seem. In a few cases, however, where the skeletal material of the new limb had connected with the proliferating periosteum of the grafted piece there was every indication that the new part was derived from the exposed proximal end. In all cases that have formed a new limb, the periosteum of the cut end of the leg-bones has formed a bar of cartilage connecting their ends with the nearest ends (the original distal ends) of the bones of the grafted piece. Two possible errors make other cases of doubtful value. The short pieces of grafted bones are often turned obliquely, or even sidewise in the end of the limb, due to the contraction of the skin as the end heals, or to changes that take place in the surrounding tissues. In most other cases, the periosteal tissue growing down from the cut end of the leg-bones passes around to one side of the grafted piece, and, with or without receiving contributions from the latter, forms the cartilage of the new limb. In fact, in some cases this can clearly be seen to have taken place, in others, while not so evident, the possibility of such a process exists and renders the result uncertain.

In order to avoid this source of error I adopted the second method of grafting described above. A long piece of the femur was grafted in a reverse position in the thigh. The length of the piece prevented its rotation, and at the same time by increasing the distance

between the distal end of the leg-bone and the proximal (now inverted) end of the graft it was possible to detect with greater precision the source of the material for the new bones. The presence of a single bone instead of two as in the former case also simplified the conditions. Despite these advantages, only a few cases were obtained in which the results seemed to show with great probability that all of the material for the new skeletal parts was derived from the exposed proximal end of the grafted piece. In such cases there was always established a cartilaginous connection between the cut distal end of the femur of the stump and the cut distal end of the grafted piece. The new limb is thus made up of a proximal piece of the femur, connecting cartilage, grafted piece of reversed femur, new tibia, fibula, tarsalia and phalanges from the proximal end of the grafted piece. Evidences of absorption are generally seen in the grafted piece. How far this might ultimately go was not determined.

Tail in Leg and Leg in Tail

By means of the skin-pocket-method it is easily possible to graft a short piece of the tail (without skin) into a pocket of the leg, and *vice versa,* a piece of the leg into a skin pocket at the cut end of the tail. I have made a few such experiments with *Spelerpes ruber* not without hopes that from the graft in the leg a tail might develop, and a leg from the end of the tail. The results proved otherwise, for, whenever regeneration occurred, the new material for a new leg came from the cut end of the old leg-bones the proliferating cells passing to one side of the grafted piece and the latter becoming absorbed.

A similar process occurred in the case of a leg grafted in a tail; a new tail and not a leg regenerated. The experiment shows that care must be exercised in interpreting the other cases where the same kind of organ is grafted in a reversed position.

Regeneration after Removing a Bone some Distance from the Cut End

In order to see what would happen if the bones are absent at the cut surface, the hind leg of Diemyctylus was cut off above the knee, the greater part of the femur was removed from the stump, and the skin sewed over the cut end. Regeneration of a new leg was delayed, but took place. The stump of the leg seemed to contract somewhat, so that the cut end of the bone was brought nearer to the cut end of the muscles. The proliferation from the end of the bone must have grown down to the cut surface, and then, extending beyond this, given rise to the material for the skeleton of the new leg. The experiment shows the possibility of the same thing occurring when a grafted piece is pushed aside. Unless the graft block the proliferation from the bones of the stump, these may contribute material to the new limb.

Attempts to Induce Regeneration in the Leg of the Frog

In order to see if regeneration could be induced in adult frogs numerous experiments have been made during three winters. Pieces of the leg were cut off, and grafted in skin-pockets in various ways, but without results. I hoped that the breaking down of such grafted pieces might incite the regeneration process, if its absence in frogs were due simply to some retarding influence in the method of closure of the cut surface as occasionally occurs in pieces of other animals that have well developed powers of regeneration.

Pieces of the leg of tadpoles (without the skin) were also inserted into the leg of the frog without inciting regeneration, but as different species were probably used for graft and stock, successful results were less to be expected. Pieces of the muscles and other tissues of the tadpole's tail were inserted in skin-pockets of the leg of the frog but without effect. Since the tail of the tadpole has remarkable powers of regeneration, it seemed

possible that the presence of such tissue might excite the leg to regenerate, but this did not prove to be the case. Possibly, here also, the difference in species spoiled the result, but this seems unlikely, since it has been shown that young tadpoles of different species may be readily united and form permanent unions.

It is well known that the skin of the frog has excellent powers of regeneration, yet when the leg is cut off it generally ceases further growth after the cut surface has healed over. It occurred to me that the pressure of the skin over the cut end might in itself prevent the further growth of the internal organs. To examine this possibility I cut off the fore-leg turned back the skin, cut off a piece of the stump, and then sewed up the end of the pocket. There was thus left a free space between the cut end of the stump and the end of the skin. Nevertheless regeneration of the limb was not hastened. In other cases agar, or the coagulated white of the hen's egg, was inserted into the pocket, on the supposition that as they were absorbed the regeneration might take place but nothing of the sort occurred. These experiments were undertaken before I became aware of the fact that the fore-leg of an adult frog may actually regenerate, but only after a long time and imperfectly, so that the experiments would be expected at most to facilitate or hasten the regenerative process which however they did not seem to do. In the winter of 1904–05 one frog that lived for several months, floating in the water, regenerated a long outgrowth from the cut end of a fore-leg. The new part had one or two rudimentary finger-like outgrowths, but although the outgrowth was long it was very imperfect as a limb. This frog had had its leg cut off twice, the second time two months after the first operation. In some preparations of Mr. Goldfarb I had seen the great thickening of the periosteum that takes place after several weeks, and this suggested, that if the leg were cut off anew at this time, regeneration might take place. I have also obtained more recently two or

three other cases of regeneration of a limb in this way, and in these the new foot was flat and broad, and plate-like, but with scant evidence of toes. That the regeneration of a new leg is not dependent on this two-fold operation has been shown by Mr. Goldfarb who has also obtained cases of regeneration of the fore-leg of the frog after a single amputation. Since Mr. Goldfarb will describe these cases in detail further description may be omitted here.

The toad, being a more primitive member of the Anura, might be supposed to have greater powers of regeneration, but experiments have been less successful with it than with the frog. The thickening at the end of the bones forms a large knob, as it does also in the frog at first, but in the toad no subsequent changes appear to take place.

Experiments with Lizards

During the summer of 1904, while enjoying the hospitality of the Marine Laboratory of the Leland Stanford University, I carried out many experiments with lizards. but since the results were purely negative they may be given in a few words. In the lizard the tail has the power to regenerate with great facility, but the legs appear to have no power of this sort. I tried grafting parts of the tail in skin-pockets in the legs, in the hope of inciting regeneration. In some cases large pieces were inserted. containing all of the tissues, in other cases pieces of single tissues, muscles, bone, periosteum, etc., were put into the pocket, but without producing the desired result. The lizards were kept alive in some cases for six to eight months without showing any signs of regenerating the leg during this time, but even the tail regeneration is not rapid. It appears, nevertheless, that the regeneration of the leg can not be induced by the presence in it of pieces of other parts of the body that have the power to regenerate.

Conclusions

Although the experiments undertaken in the hope of inciting regeneration in parts that do not do so ordinarily, or imperfectly and only after a long time, have not given any positive results as yet, still even the negative results are not without a certain theoretical interest. The experiments with the frog showed that the lack of power to regenerate, or only to regenerate imperfectly after a long time, is not due to the pressure of the skin on the cut end of the parts beneath. It is interesting to find that when after several months the internal parts begin to push out a new stump, as sometimes occurs, the skin is then also incited to regeneration, and will form a suitable covering for the parts beneath. It is plausible to suppose that this growth of the skin is due to the pressure of the new part from within. Other factors may also enter into the result, but that the pressure must be the main factor is shown by the failure of the skin to regenerate when other tissues, those of the tail for instance, are present, that have themselves the power to regenerate, but not finding suitable conditions for regeneration fail to form an embryonic knob. In its absence the skin is not incited to regenerate. The fact that the skin does not show any tendency to complete itself alone, although it has the power of regeneration, is important as showing that the possession of this power is not itself a stimulus that will lead to its development. Some other condition is necessary to call it forth, and in this case, that condition seems to be pressure from beneath.

Other tissues in the leg may also have the power to regenerate, but fail to do so unless certain conditions are realized. This state of affairs may lead us to hope that with a better knowledge of the conditions we may ultimately control them, and I trust this may be a first contribution towards that end.

That the muscles in the frog's leg have the power to

regenerate can be shown by cutting from the side of the gastrocnemius a square piece of muscle tissue. In the course of a few months I have found that the muscle regains its size, which seems to be due, in part at least, to the formation of new muscle, although hypertrophy of the remaining fibers may also assist in the enlargement.

There is some indication that the delay in the formation of the new leg in the frog is due to conditions existing in the bones or muscles and, as I have pointed out,[1] it is significant to find that in the vertebrates the loss of power to regenerate a limb appears where cartilage has been changed to bone. The result is not however due directly to the ossification, since the new material is derived from the periosteum and not from differentiated tissue.

Especially interesting is the evidence showing that the introduction of material, itself capable of regeneration (as when the tail-tissue of the lizard is introduced into the leg-pocket) does not incite the leg to regenerate. If the process of regeneration is due to some enzyme, or other substance of this nature, that arises in an injured region, and whose presence incites the new growth, we might hope by introducing pieces of material capable of forming such substances to incite regeneration, but no such result followed. It would be unwise to lay too much weight on negative evidence of this kind, but the results as they stand indicate, perhaps, with some probability, that the primary cause of regeneration is not to be found in this direction.

Finally, to revert once more to the experiments that gave positive results. It has been shown that from the proximal end of a reversed femur new limb bones develop. This result calls for further analysis. It is clear that each level of the limb has the power to regenerate all of the parts lying more distal to it, and in all proba-

[1] The Harvey Lectures for 1906–7.

bility every level has potentially the power also to regenerate all the other parts of the limb proximal to that level. It is difficult to show that a distal part has the potentiality to produce more proximal parts, but the facts make this interpretation highly probable. How much of the distal end regenerates depends in part on its relation to what is left in the stump, and in part on the necessity of forming a distal structure. Between these limits the intermediate parts are laid down. The proximal cut end of a limb must have the same potentiality of forming distal structures as has a distal end and in those cases where the possibility exists of forming either an anterior or a posterior structure, as in pieces of lumbriculus, for example, some other relation must determine that from one end of a piece a head always develops, and from the other end a tail. I have suggested that the direction of the gradations of the old material (as expressed in their differentiation) is the factor that regulates this result. If we apply these same ideas to the special case under consideration we might expect the proximal end of the leg (or any part of it) to regenerate only proximal structures; in other words to complete the proximal end of the femur and produce a scapula at the exposed end of the leg, and, theoretically, one might imagine the further development of a salamander around the scapula as a center. The facts are the reverse. The conditions that determine in the case of the reversed femur what shall regenerate of the various possible ones are not so simple as just described. In the first place, the detachment of the femur from the rest of the limb may soon lead to changes in it that cause it to lose that gradation of materials on which the polarity of the new part depends. There is also the possibility that the polarity of the other tissues may have a counterbalancing influence. But far outweighing these possibilities there is another consideration of greater weight. The special group of tissues found in such an organ as a limb may be capable of forming only one

structure, if they form anything at all, namely, a leg, and not a salamander to take the extreme case. But why always the distal end of the leg and not the proximal, *i. e.,* not femur and scapula? The determination of the distal end rather than the proximal must be due, I think, to the presence of the free rounded knob covered by the new skin which gives the stimulus for a distal structure, and the foot end of the leg is the only possible distal structure that exists for this organ.

The case is parallel to the formation of a heteromorphic tail in the earthworm, that develops, as I have shown, from the anterior end of a piece when cut behind the level of the twentieth segment, or thereabouts. Here also a distal structure develops, but the nature of the material is such that a tail rather than a head regenerates. While polarity, as an expression of the gradation of the materials, is one of the factors that determines a result, it is not the exclusive factor. In Lumbriculus a head forms at the anterior end of a piece at nearly all levels and a tail at the posterior end. Here we must assume that the kinds of materials are so equally balanced throughout the greater length of the worm that the polarity determines the result, while in the earthworm and in the leg of the salamander another condition determines a different result. In the latter cases the kind of material, or the organ-complex, makes it possible for only a tail or a leg to develop at either end of the piece, and the presence of a free end determines that its new structure must be the terminal part, hence a foot in the case of the salamander, and a tail in the case of the earthworm, is regenerated even from a reversed end.

THE PHENOGAMOUS PARASITES

By DR. CHARLES. A. WHITE

Smithsonian Institution

The object of this essay is to describe in a popular manner the chief characteristics of the known kinds or groups of phenogamous parasites, to show their relation to one another and to normal phenogams, and to discuss their structure and habits with reference to the probable manner of their origination. In order to make a popular statement of the characteristics of each group of these abnormal plants and to discuss them clearly it is first necessary to summarize briefly the elemental structure and physiological characteristics of the normal phenogams. I have chosen to do this in verbal terms a part of which are somewhat unusual, but which are believed to be specially appropriate to discussions of this kind.

The elemental parts of a normal phenogamous plant are root, stem and leaves, the beginning of the differentiation of which structures is distinguishable even in the embryo; and to these are added, at the maturity of the plant, flowers and fruit. Every normal phenogam also consists of two incremental parts, an up-growing and a down-growing part, respectively, the latter entering the soil to form the roots. The normal phenogamous plant performs all its physiological functions within, and for, itself and lives independently of all other plants except in the matter of competition with them for the benefits of soil, moisture and sunlight, but the parasites escape the performance of those functions so far as nutrition is concerned. The normal plants derive the materials for their subsistence and growth from inorganic sources and elaborate them within their own tissues for their own use, producing thereby their new organic substance, but the parasites rob other plants of that substance in its elab-

orated condition. The supply of inorganic material is obtained by normal plants partly in a soluble and partly in a gaseous condition, the former being contained in the food-sap which the roots derive from the soil, and the latter in the atmosphere which surrounds the plant. The function of the root requires a constant accession of moisture, and that function is vital with relation to the other functions of the plant presently to be referred to. The action of sunlight is indispensable in the condensation and elaboration of those inorganic materials into new organic substance. An essential step in that elaboration of new material is the production of chlorophyl, which takes place partly in the bark of the growing branches, but mainly in the parenchyma of the leaves. Fully developed green leaves are therefore among the chief organs of normal phenogams, and their absence from the greater part of phenogamous parasites is due to the inability of those plants to produce chlorophyl. It is for these reasons that chlorophyl is so frequently mentioned in the following paragraphs.

The reproduction of normal phenogams is by two methods, namely, parturital [1] and blastemal.[2] These methods have such relevancy to the subject in hand that it will be frequently necessary to refer to them. The first is the conjugative method and provides for the hereditary transmission of specific and other systematic characters, the geographical distribution of species and the multiplication of individual plants. It is periodically cyclic, the maturation of the seed ending one cycle and the germination of its embryo beginning another. The second is the autogenous method and pertains to the growth and preservation of the individual plant. Its operation is physically continuous during the whole life of the plant, and every bud of the plant is connected with all the other buds by living somatic cells. The horticultural processes of budding and grafting consist of transferring blastemal

[1] Parturio, to bring forth young.

[2] Βλαστος, a bud. These terms are regarded as preferable to "sexual," "asexual," "vegetative," etc., which are often used by writers.

reproduction from one plant to another. They are closely simulated by some parasites in their manner of attachment to the host, but there are radical differences between parasitic attachment and horticultural grafting.

The two incremental divisions of every normal phenogam consists of an epitropic, and an apotropic[3] portion, respectively, separated by the tropaxis. The epitropic portion, beginning with the radicle at germination, enters the ground, divides into roots and rootlets, and establishes the plant in position. This is primary epitropism. The apotropic portion at the same time extends upward, forming the stem and finally the branches, leaves and fruit. This is primary apotropism. The tropaxis is a theoretical disc at, or a transverse section of, the base of the stem from which growth proceeds in opposite directions. Its functional existence as a dividing plane is real and constant during the life of the plant, but it is structurally not clearly definable. That is, no material change of plant-texture occurs at the place where the upward and downward growth diverge, and no obstruction to the flow of food-sap from one to the other portion exists there. Suckers, stolons, sprouts, etc., sometimes spring from roots, root-stalks or tubers, and become new plants. This is secondary apotropism. Roots or rootlets often spring from the stem or branches. This is secondary epitropism. A new or secondary tropaxis is formed in every case of secondary apotropism at the place where the upward growth begins and new roots turn down into the soil.[4]

Such are the leading structural characteristics of normal phenogamous plants, which constitute the mass of

[3] For a full explanation of these and some of the following terms see my article in *Science*, N. S., vol. XII, pp. 143–146.

[4] The terms "hypocotyl" and "epicotyl," meaning below the cotyledons and above the cotyledons, respectively, often have been used by authors to designate the apotropic and epitropic portions, respectively, of the germinating embryo. Those terms are inappropriate for such use because the place of attachment of the cotyledons rarely, and only accidentally, coincides with the place where upward and downward growth diverge, and the two places are often far apart. A case in which they are far apart is illustrated by the plantlet of Convolvulus as shown by Fig. 6, on page 28.

the green vegetation of the earth. Abnormal phenogams constitute only a very small proportion of the great mass of vegetation, and yet the aggregate number and variety of their forms is really very great. Three general kinds of abnormal phenogams are recognized, namely, parasites, saprophytes and symbionts. They have certain characteristics in common and often are visually similar, but they differ materially from one another in the manner of procuring their subsistence, and the habit of each of them in that respect may be either partial or complete. That is, a phenogam may be partially parasitic, saprophytic, or symbiotic, and partially normal; or parasitism may be associated in one and the same plant with saprophytism. While my chief object is to discuss the parasites, it will aid in defining their characteristics to present a brief statement of those of the two other kinds of abnormal phenogams.

Saprophytes derive their subsistence from dead organic matter in the soil which has not reached the stage of full decomposition. That matter yields a soluble portion to the food-sap which the plant obtains by its roots in the usual manner and, after some reelaboration, that portion is applied by the plant as new organic substance in the building of its tissues. Saprophytes, like vultures, hyenas and epicures, take their food in a partially decomposed condition and thrive upon it. Doubtless many plants that are properly regarded as normal are really in part saprophytic when their roots have access to organic manures, but only completely saprophytic phenogams are here referred to. It is claimed by some investigators that completely saprophytic phenogams sometimes produce chlorophyl and develop green leaves, but those here discussed produce no chlorophyl, develop no functional leaves, and are therefore not green in color. Their reproduction, both parturital and blastemal, is normal and they grow from their roots in the soil like normal plants, with none of which are their vital relations antagonistic. Completely saprophytic phenogams, which only are now particularly referred to, are comparatively rare, especially in ordi-

nary soils. They are mostly confined to swampy and other moist soils that contain much decomposing vegetable matter, and to shady positions. It may be suggested that the abundance of disintegrating organic material contained in the soil in which these completely saprophytic plants grow furnishes so large a supply of material which is still useful for assimilation in the production of new organic substance that the entire leaf-function, including the production of chlorophyl, is suspended as being superfluous, and that this habit has become permanent and hereditary.

Completely symbiotic phenogams live in enforced vital union with a fungus which adheres to and covers its roots, and through which it derives all its soil-subsistence. The roots being entirely enveloped, their normal function is destroyed and the fungus also assumes the office of purveyor of nutriment. As do other fungi, it obtains that food-material from decomposing organic matter in the soil and transfers a portion of it to its consort through their surfaces of contact. Although that food-material, when obtained by the fungus, is partially decomposed, and is received at second hand by the captive phenogam, the latter thrives upon it, and, its above-ground portion being free, the functions of vegetative growth and reproduction are normally performed. Its leaves, however, are abortive or functionless and never green in color, for completely symbiotic phenogams do not, and do not need to, produce chlorophyl. Their failure to do so is doubtless a direct result of the condition which is imposed upon its roots by its fungus consort. The vital relations of these strangely modified phenogams with other plants are normal, but their condition with relation to the fungus is apparently that of pitiable captivity. The usurpative control of their nutrition by the fungus suggests that these phenogams did not originate as symbionts by a predilective departure from a self-supporting condition. Partial symbiosis of fungi with phenogams is not uncommon and is understood to be, at least in many cases, mutually beneficial, but it has only incidental relevancy in

this connection. One can hardly doubt that the complete symbiotic condition of those plants has been imposed by the aggressive increase of the fungus from its original condition of partial symbiosis, but the phenogam so fully acquiesces in it that the deficiencies of structure and function which its imposed condition entails have become harmonious with that condition and hereditary. Even the embryo, at least in the case of Monotropa, or Indian pipe, and probably also in that of Sarcodes, or the snow plant of California, has lost its differentiation into cotyledons and plumule. This is a significant coincidence with a similar condition which prevails in the embryo of many parasites, as will be shown in following paragraphs.

Examples of complete symbiosis are few among phenogams, the most common case being that of Monotropa. All the older botanists believed, and some of them so stated in their text-books, that the species of that genus are parasitic upon the roots of woody plants. Later authors often have stated that Monotropa is saprophytic, but still later investigators have demonstrated that the plants of this genus are completely symbiotic. It will be a disappointment to the older plant-lovers not to find their familiar acquaintance, the Indian pipe, discussed among the parasites on the following pages, but the facts which have been stated require its omission there.

Whatever view one may take concerning the two kinds of abnormal phenogams that are briefly defined in the preceding paragraphs, he instinctively regards the parasites as a criminal class in the great community of honest plants. Their methods of parasitism are so varied, and each method is prosecuted with such vigor and constancy, that it is necessary to review them with reference to those habits rather than to similarities and differences of systematic structure. They all are at least acquisitive in their relations with other plants, and some of them are vigorously aggressive and raptorial. They all derive new organic substance from other plants, always from living ones, and apply it directly in the building of their own tissues. Some of them are annual, and some

perennial. Some are herbaceous, and some woody. Some of them attack only the epitropic, and some only the apotropic, portion of their host. Some are only partially parasitic, obtaining only a part of their subsistence in that manner, but a large number are completely parasitic, and thus obtain their entire support from other plants. The former obtain a part of their subsistence from the soil as normal plants obtain all of theirs. They also develop leaves and produce chlorophyl, but the complete parasites, with exceptions to be mentioned, develop no functional leaves and produce no chlorophyl, for completely parasitic plants do not need to produce it. New organic substance, elaborated as already has been mentioned, is of course necessary to the existence of the normal plants which produce it. It is no less necessary to the existence of the parasites, but they, not being able, or not predisposed, to produce it for themselves, obtain it by robbery from other plants. All of them are so depraved that they acquire special hereditary habits of rapine, modify their structure, and even develop special organs with which to accomplish their thefts. The deficiencies and modifications of structure are correlated with the respective kinds of parasitism, and they are invariable and heritable. Even the embryo of some of them is structureless, not being differentiated into cotyledons, radicle and plumule. Indeed, some of the most vigorous of the parasites originate from embryos that apparently represent only a moiety of the normal phenogamic embryo.

The leaves of normal phenogams are properly regarded as the chief organs concerned in the production of chlorophyl, but if my assumption is correct that the agency of a structural root is a precedent necessity in normal cases of such production, the functional leaflessness of a parasitic phenogam is a direct consequence of its rootlessness. That is, because a rootless phenogam can produce no sufficient quantity of chlorophyl, and because it procures its new organic substance by theft, it has no use for leaves. Therefore, those leaves which it morphologically inherits remain undeveloped or functionless. This is the

condition of complete parasitic phenogams, but those which are only partially normal supplement their honest gains by theft. They are all robbers, and obtain new organic substances from their hosts by methods which resemble grafting, budding and leeching, respectively. In the first two cases mentioned the embryo of the parasite is thrust into the living tissue of the host from which the resulting parasitic plant draws its nourishment, much as do the bud and scion in cases of budding and grafting. In the other case special organs, namely, haustoria, are developed as instruments of robbery. These organs serve to draw new organic substance in liquid form from normal plants, and they are as indispensable to the parasite which possesses them as are roots to normal plants. They are produced as small outgrowths from different parts of different parasitic species, sometimes upon the roots and sometimes upon the stem and branches. They are of wart-like, discoid, globular, or more or less irregular form, and are sometimes single and symmetrical, but oftener in groups or clusters and shapeless masses. When single they are sometimes sessile and sometimes terminal on slender pedicels. They attach themselves by their free surface to the host, and so burrow into its subcortical and subcortical tissues that the growing cells of both plants are intimately commingled. Acting like suckers, they withdraw in liquid form the new organic substance which the host had prepared for its own use, much as a leech extracts blood from its victim. The haustoria of parasites are comparable with roots of normal plants because, like roots, they are the instruments by means of which the plants obtain necessary supplies, but true haustoria are not roots nor morphological representatives of them.

The foregoing remarks apply mainly to the general characteristics of the parasites as compared with saprophytes, symbionts and normal plants. The special characteristics of the parasites are grouped and briefly summarized in the following synopsis. In remarks which follow each synoptical statement some of the more con-

spicuous of those extraordinary habits which members of the various groups possess and which have become constant and hereditary will be shown. Many of those habits are of wonderful character, and one almost feels that he is dealing with sentient beings of great cunning and lawlessness rather than with vegetal forms.

The phenogamous parasites are so aberrant as regards both their structural and vital relations to other plants and to one another that it is difficult to classify them. Indeed, there is no logically recognizable correlation of any of the parasitic characters of the species in question with those which pertain to systematic classification. The following synopsis, prepared for the present occasion only, embraces seven groups the characterization of which is, so far as practicable, based upon the manner of parasitism of the members of the respective groups and upon the peculiarities of their life history, especially that phase of it which pertains to germination.

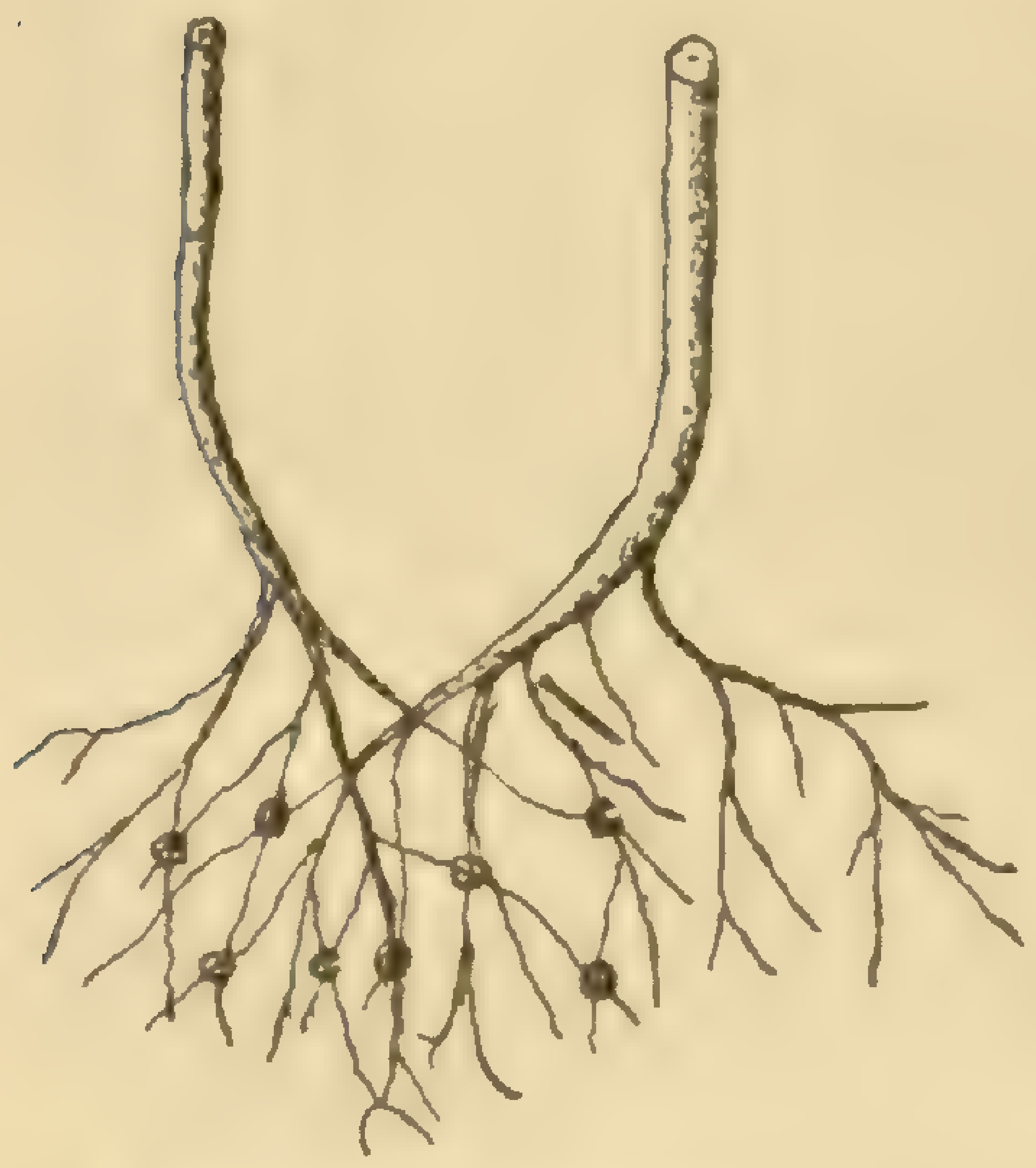

FIG. 1. Diagrammatic pen-sketch, showing the position of haustoria at the places of contact of roots of the parasite and its host. The haustoria are represented by small circles, which are, however, proportionally much larger than natural size.

GROUP I

Seeds germinate upon the ground. Embryo differentiated into cotyledons, radicle and plumule, like normal embryos. Like normal plants also those of this group produce chlorophyl. A part of their roots are attached by sessile haustoria to roots of other plants, from which they obtain ready-made organic substance in liquid form, and a part of them obtain food-sap from the soil in the normal manner. Therefore their parasitism is only partial. Examples: Euphrasia, Pedicularis, Castilleja and many others.

The parasitism of the members of group I, which are

mostly perennial herbs, is confined to limited underground pilfering. It is the simplest form of phenogamous parasitism but it is as persistent and hereditary as are the more complex forms, and it is practised by a large number of genera and species which have numerous near normal relatives. Because they have normal roots and leaves and produce chlorophyl they begin life with the ability to procure an honest living, but they seem to be unable to resist their inherited parasitic inclinations. The development of haustoria at the points of contact of their roots with roots of other plants begins after their germinative birth from a normal embryo and an early stage of full self-support obtained from the soil; but so firmly fixed is the habit of pilfering in these plants that when they have been experimentally forced to live honestly in good soil, but beyond the reach of roots of other plants, they have ceased to thrive, as if they were insufficiently nourished.

Group II

Parasites attached to the stems and branches of woody hosts upon the bark of which the seeds germinate, being affixed there by their glutinous covering. Embryo differ-

Fig. 2. Pen-sketch of a branch of *Viscum album*, the Old World mistletoe; much reduced in size. *A*. Diagram showing the mode of attachment of the parasite to the host by the sinkers.

entiated into cotyledons, radicle and plumule, and the plant consists of both epitropic and apotropic portions. The latter is differentiated into stem, branches, leaves and fruit, as in normal plants. The leaves, and also the bark of the stem and branches, contain chlorophyl which is produced by the plant itself. The parasite is attached

to the host by "sinkers" which consist of specially modified, but true, rootlets, although in function they simulate the haustoria of other parasites. The sinkers penetrate the bark of the host and obtain nourishment for the parasite from the growing tissues beneath it, much as food-sap is obtained from the soil by normal plants. The parasitism is complete. Examples: The mistletoes.

The members of group II are perhaps the most generally known, at least by name, of all the phenogamous parasites. The family to which they belong, the Loranthaceæ, is a large one, and some of its members differ considerably from the typical forms of mistletoe. Only *Viscum album* of the Old World, and *Phoradendron flavescens,* of the New, however, are chosen to represent group II on this occasion. These mistoes differ from the members of all the other parasitic groups in being perennial woody parasites upon woody hosts, and also in their method of parasitism. That method is peculiar because it simulates grafting, because morphologically its "sinkers" are true rootlets and not haustoria, and because the passage of sap from host to parasite is by those rootlets and not through such harmoniously joined cells as are formed between the graft and its stock. Mistletoes have been known to become parasitic upon other mistletoes, but in their choice of a host they usually give preference to trees that are not botanically related to them. Their structure, both embryonal and mature, is so nearly normal that one might believe them capable of

Fig. 3. Pen-sketch of a branch of *Phoradendron flavescens,* the New World mistletoe; two fifths natural size.

leading an honest life in the soil, but so firmly is their predatory habit established by heredity that they never do so. Their seeds will germinate successfully only on the bark of living trees, and their embryos, although structurally perfect, are evidently unable to develop in the soil. When germination of the seed begins the radicle pierces through the dry bark of the host as if driven by some extraneous force; and it sometimes enters the bark of a branch from its under side, showing that gravity is not that impelling force. It lifts the strong bark by its increment beneath, and sends the sinkers into the growing layers. The cells of those layers and the cells of the sinkers become vitally commingled much as do the somatic cells of the scion and stock in common grafting, but not quite so harmoniously. This parasitic root-grafting is remarkable because the parasites and their usual hosts differ from each other in botanical relationship far more than do any scions and stocks that can be artificially grafted with success.

Because the mistletoes obtain full nourishment from their hosts their parasitism is complete, and yet, unlike other completely parasitic phenogams, they produce chlorophyl in their own tissues. The production of chlorophyl by the mistletoes is apparently due to the fact that they have retained morphological representation of true roots, notwithstanding their parasitism. While the mistletoes have retained more of the structure and functions of normal plants than have other completely parasitic phenogams, their draft upon the vitality of their hosts is great, and it doubtless would be more apparent if the latter were less vigorous.

Group III

Seeds, having the embryo differentiated into cotyledons, radicle and plumule, germinate upon the ground and there produce plants which begin to grow in the soil in the normal manner. By their earlier roots they are partially parasitic after the manner of group I, but, suddenly, the whole plant becomes epitropic and enters the soil bodily by burrowing, much as does the peanut pod

when ripening. It there branches freely, assuming the form of a large complex blanched rootstock, and becomes wholly parasitic. It passes its whole mature life under ground except that some of its branches rise above ground to flower, but those branches always die when the fruit has ripened. Its earlier parasitism is by sessile haustoria, which are soon discarded, and its later parasitism is by haustoria-tipped tendrils, sometimes erroneously

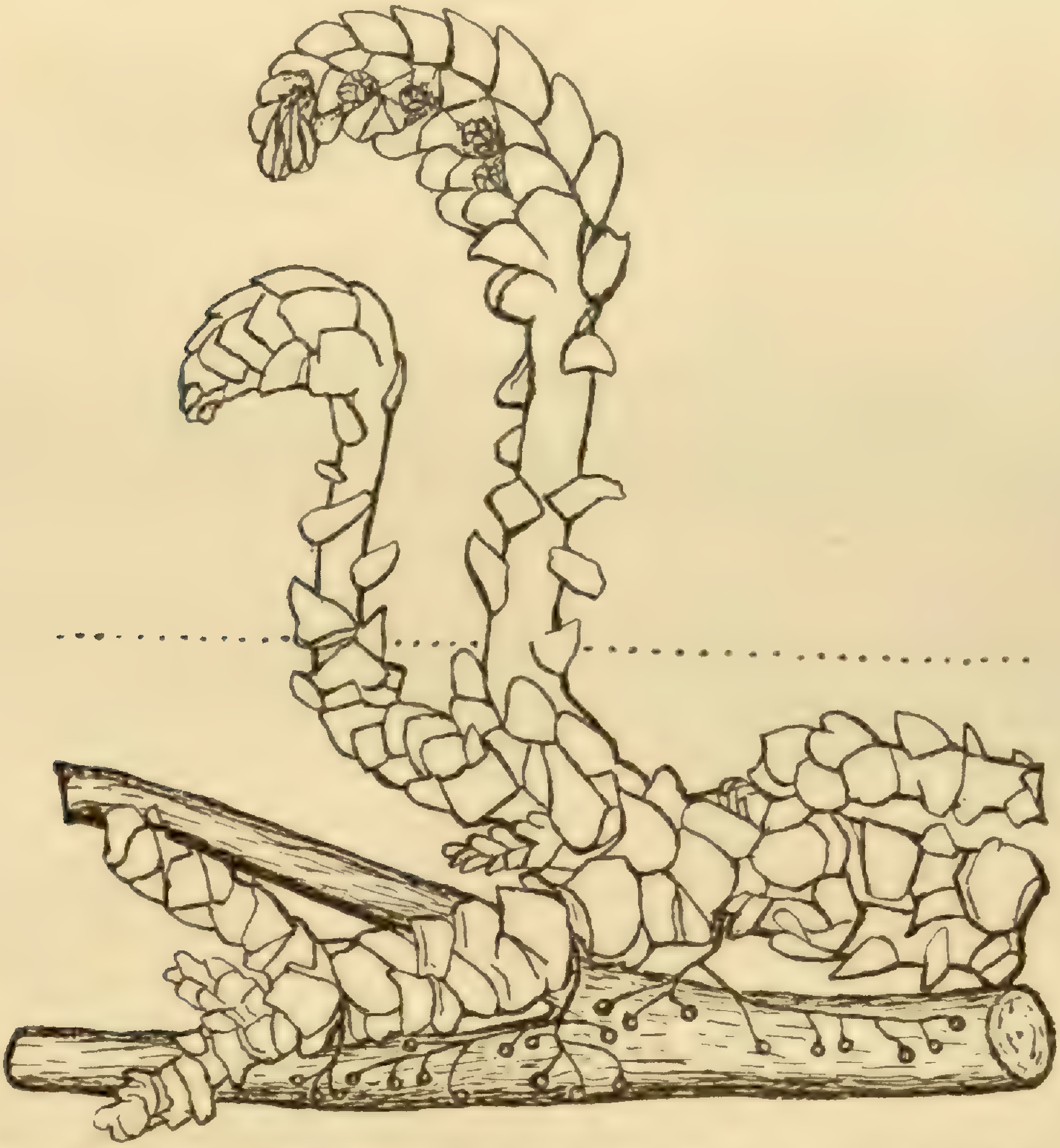

FIG. 4. *Lathræa squamaria*; pen-sketch after Kerner. The dotted line represents the surface of the soil. Only a small part of the underground stems and branches is shown in the figure, together with tendrils bearing the pediculate haustoria.

called roots or rootlets, which issue from the underground stem and branches. No chlorophyl is produced and no functional foliage or functional roots are developed after the plant begins its burrowing. Example: *Lathræa squamaria*. This group has no known American representatives.

The species which has been chosen to represent group III is a European form and is quite distinct in certain respects from even its nearest botanical kindred, and it possesses habits that for variety and extent of abnormality are not surpassed, and apparently not equalled, by any other plant. It begins life normally, as do members of group I, which it then closely resembles. The presence of chlorophyl in the plumule of its plantlet and the development of early rootlets seem to indicate an honest destiny for the plant, but its subsequent acts almost suggest its utter abandonment to a groveling life.

Group IV

Seeds germinate upon the ground, producing an annual herbaceous plant. Embryo filiform and coiled within a mass of albumen in the seed; not differentiated into cotyledons, radicle or plumule. The resulting plantlet retains the filiform structure of the embryo without differentiation, except that the part which becomes the lower end of the plantlet is slightly enlarged. As the embryo uncoils the larger end enters the ground a little, but sends no rootlets into the soil and therefore derives no true food-sap therefrom. The smaller end points upward and the plantlet elongates as a single thread-like stem until it comes in contact with some freshly growing part of another plant. It there attaches itself by quickly developed haustoria, derives from the helpless host its first sufficient nourishment, and becomes a branching vine. It then reaches out for other hosts by more or less numerous branches, and the part below the first haustorial attachment quickly withers and dies. The branches grow rapidly and bear an abundance of flowers and seed. The plant never naturally produces chlorophyl, and develops neither true roots or functional foliage. The parasitism is complete. Examples: Cuscuta of many American and European species, and Cassytha of many Australian, New Zealand and East Indian species.

The members of groups I, II and III are all developed from perfect embryos, like those of normal plants, their

parasitism and abnormal structures being developed after germination. The remaining four groups are not only deficient in structure at maturity, but they originate from embryos which are also deficient in structure. The first of those four groups to be considered is especially represented in our country by the genus Cuscuta which contains many species, commonly known as dodder. They are often found growing plentifully in fields, thickets and waste places during the summer months, their yellowish tangled masses making them conspicuous among the green vegetation. The embryo of Cuscuta gets very little sustenance from the albumen which envelops it in the seed because the seeds are small; and it is because the plants develop no roots that they get no real nourishment from the soil. Nevertheless, the plantlet grows rapidly, somtimes to several inches in length, before it reaches a host; and although it is so slender it possesses great vegetative vigor. This vigor is conspicuously observable in the subsequent growth of those species which often profusely festoon shrubbery, and even trees, securing their hold upon, and their sustenance from, the tender twigs by means of their haustoria. Other species no less vigorously attack the smaller plants and field crops with which they come in contact.

FIG. 5. *Cuscuta Europæa;* parasitic on a hop vine. Sessile haustoria are shown at places of contact of parasite and host.

The parasitism of Cuscuta differs from that of the other groups in being effected by climbing as a vine from plant to plant, and by lateral haustorial contact of the stem and branches of the parasite with those of the host. In the case of the other groups whose parasitism is aboveground the success of the depredating plant depends upon the propitious position which the seeds may accidentally

obtain; but the plantlet of Cuscuta, after its germination upon the ground seems, by the movements of its free end, to start out in search of opportunities. It adjusts its mode of life to prevailing conditions by delaying its own germination about a month later than that of its prospective victims of annual growth, and it is not discouraged by failure of its first effort to find a host. In that case it falls down upon the ground, shriveled and apparently dying, but if soon, or even within a few weeks, some belated normal plantlet should spring up near it, or some growing branch should droop and touch it, the victim is quickly seized upon by the apparently dying plantlet. Such tenacity of life and apparently dominant purpose in a slender, organless mass of vegetable cells is no less than marvelous.

Because the plantlet of Cuscuta develops no root or rootlets it evidently possesses no real representation of the epitropic portion of a normal plantlet, or at best, not more than a moiety of it which lies immediately subjacent to the tropaxis. The rapid upward growth of the filiform plantlet indicates that at least a considerable part of the apotropic portion is therein represented. Moreover, because it has no cotyledons or plumule it follows that the entire plantlet of Cuscuta represents only the stem of the normal plantlet, or that portion of it which comes between the cotyledons and the uppermost rootlets. The accompanying diagram, Fig. 6, illustrates the foregoing statement.

The upper end of *B*, Fig. 6, not reaching above the upper dotted line, indicates that the plantlet of Cuscuta possesses no representative of either cotyledons or plumule. Its downward extension a little below the lower dotted line similarly indicates the fact that its lower end enters the soil a little way, but that it does not represent enough of the epitropic portion of the normal plant to give origin to a root, or any rootlets. This comparison shows that the whole plantlet of Cuscuta represents only the stem of the plantlet of Convolvulus.

The descriptions which have been given in the preced-

ing paragraphs of the structure, germination, life habits and method of parasitism of Cuscuta apply in every important detail to Cassytha. Even the general aspect of the latter plants is such that an American or European seeing them for the first time instinctively regards them as dodders. Nevertheless the structure of their florescence and fruitage leaves no room for doubt of their close

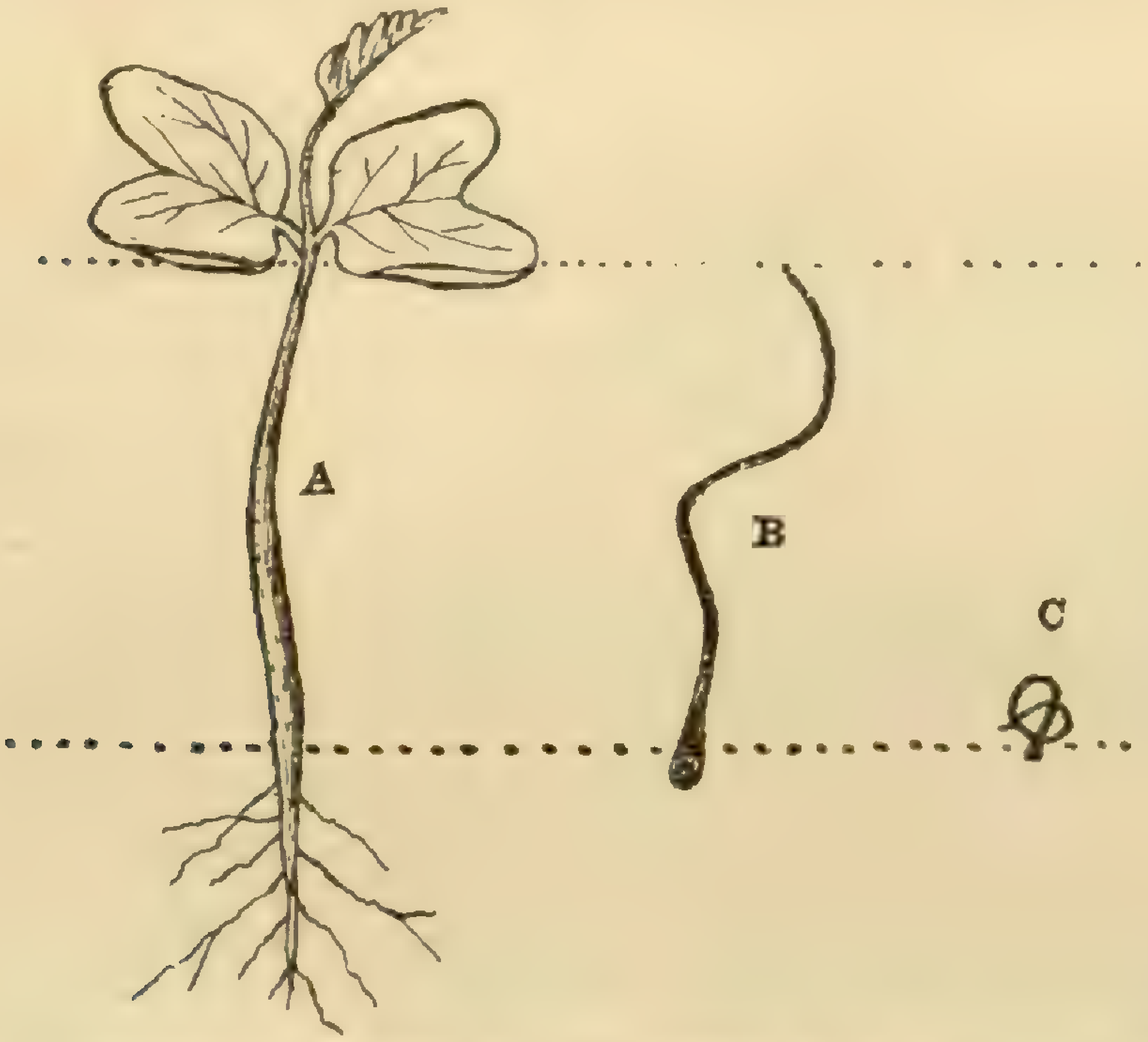

FIG. 6. Diagraphic illustration of the relation of the embryo and plantlet of Cuscuta to the plantlet of Convolvulus.

A. An early plantlet of Convolvulus, with its first root and rootlets, its stem, cotyledons and the first leaf of the plumule, not yet expanded.

B. The filiform plantlet of Cuscuta of nearly the same stage of growth from the seed as *A*.

The upper dotted line crosses *A* just a little below the place of attachment of the cotyledons. The lower dotted line represents the surface of the soil and also the position of the tropaxis of *A*.

C. Embryo of Cuscuta, at the beginning of germination. Much enlarged.

relationship to the Laurel family, while all the species of Cuscuta are nearly related to the Convolvulaceæ.

GROUP V

Seeds germinate upon the ground. Embryo filiform and not differentiated into either cotyledons, radicle or plumule. Its protruding end, or offshoot, penetrates the soil after the manner of a radicle, sometimes to the depth of several inches, but as it sends off no rootlets it derives no true food-sap from the soil. The upper end, or that

which in the normal embryo would bear the plumule, is not developed. If the descending end comes in contact with no living root of another plant the whole embryo dies, although the soil may be abundantly fertile. If it reaches such a root it becomes attached to it and develops a tuberous mass at the place of contact. From this mass spring outgrowths which penetrate the bark of the root-host and blend intimately with the growing layer beneath it, where they act as haustoria. In this mass, also, by a kind of blastemal germination, buds, or substituent plantlets, are formed which produce the flowering stems. No functional foliage and no true roots are developed, and no chlorophyl is produced.

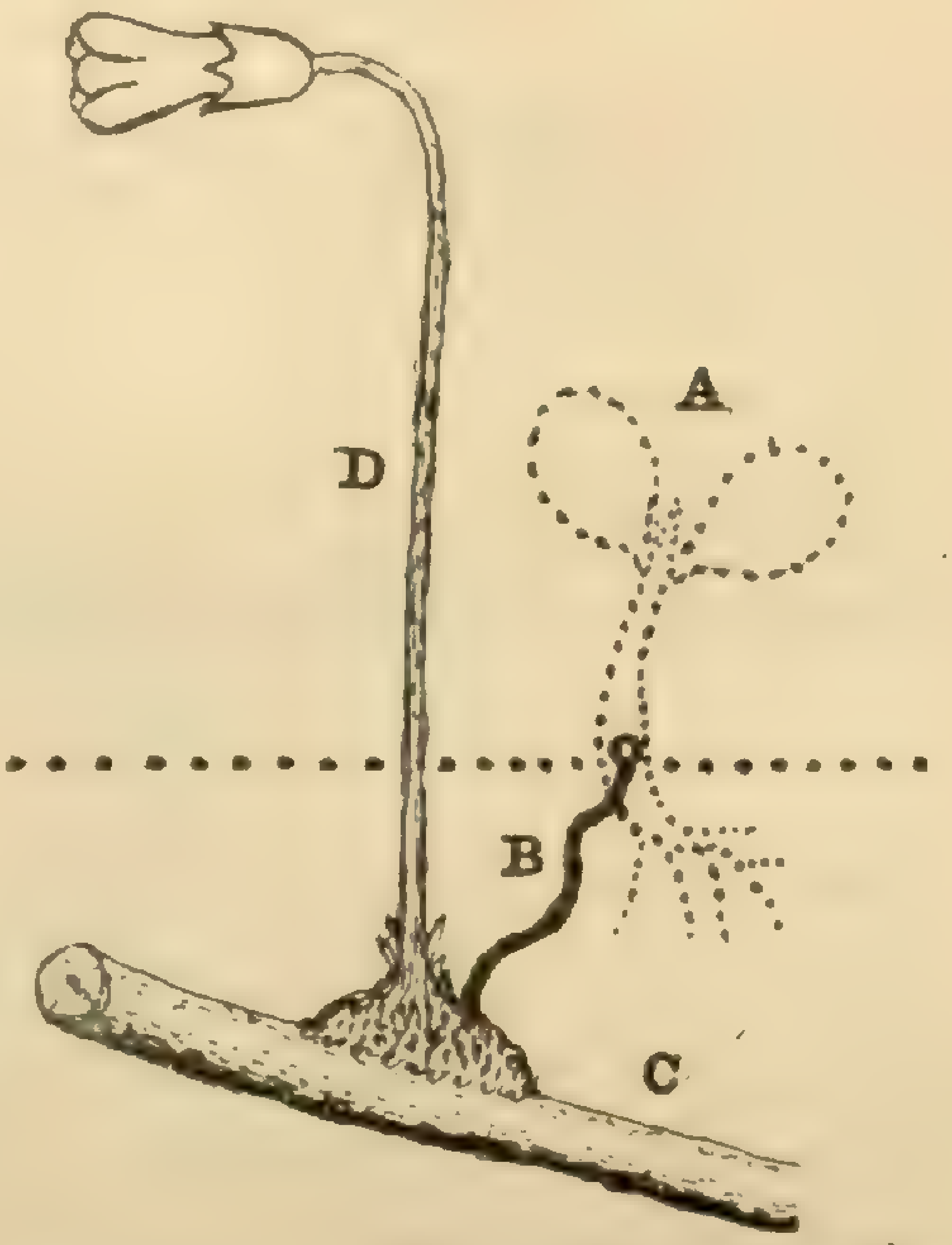

FIG. 7. Diagraphic illustration of the manner of germination and florescence of the broom-rape family, and of the structural relation of its embryo to the normal dicotyledonous embryo.

A. Dotted outline of a normal plantlet introduced only for comparison.

B. Offshoot of a broom-rape embryo. The upper moiety only may be regarded as representing any part of a normal plantlet, and that represents a portion of the stem. The lower portion of the offshoot is spirally prolonged underground, its free end becoming attached to the root-host by a tuberous enlargement.

C. The root-host.

D. Flowering stalk of *Aphyllon uniflorum* springing from the tuberous end of the offshoot. The horizontal dotted line indicates the surface of the soil.

The parasitism is complete. Examples: the broom-rapes and related genera.

The parasites of group V belong to the Orobancheæ, the broom-rapes being chosen as typical members. They are vigorous in their growth and aggressive in their parasitism, some of them being very destructive of cultivated crops; especially hemp and tobacco. Like Cuscuta they delay their own germination until their prospective victims have germinated and grown sufficiently to serve their purpose. The seeds of those species which are parasitic

upon cultivated crops seem sometimes to remain in the soil without germination more than one season, and to germinate when a new cultivated crop is planted. The accompanying figure represents the manner of germination of a member of group V and the growth of its flower stem.

Figs. 5 and 7 respectively represent two parasitic plants which, although they originate from physically similar embryos, are so widely different in their mature structure and habits that the following comparison is thought to be desirable. The seeds of both these parasites germinate upon the ground, but the resulting plantlet of one of them grows upward and that of the other downward, in search of a host. The plantlet of Cuscuta grows upward, which is attributed to the assumed fact that its embryo possesses a considerable representation of the apotropic portion of a normal plantlet, and little or no representation of the epitropic portion. No part of the broom-rape embryo grows upward, presumably because it possesses no representation of the apotropic portion of a normal embryo. Its whole embryo seems to represent only a moiety of the stem of a normal plantlet which lies subjacent to its tropaxis and above its rootlets. The bud from which springs the flowering stalk of broom-rape is not a part of the embryo proper, as is the plumule of the normal embryo, but a result of secondary germination.

Group VI

Seeds germinate only above ground and, like those of the mistletoes, only upon a living woody host; usually upon the stem and branches, but sometimes upon exposed roots. Embryo filiform and without either cotyledons, radicle or plumule. No true roots or functional foliage is developed, and no chlorophyl is produced. The embryo, by its distal or protruding end, when emerging from the seed, sharply and vigorously penetrates the bark of the host and sends haustorial processes into the cambium layer, and even into the alburnum. A single flower, some-

times sessile and sometimes having a short stem, issues from the host at the place of entrance of the embryo. The parasitism is complete.

Examples: The rafflesias and related forms.

One of the most remarkable characteristics of group VI is that the individual plants of many of its species reach the lowest structural limit of the phenogam. That is, each one of such plants consists of a single flower which is sessile upon the bark of the host, or apparently sometimes upon its cambium layer. In other cases the plant consists of a short, single scaly stem besides the flower. The sessile species are examples of flowering plants reduced to the flower alone, assuming that the haustorial processes at its base represent the torus, as they seem to do. While the normal phenogam consists of root, stem and leaves, all of which are necessary to serve the purpose of the coming flower and fruit, the sessile Rafflesias throw the responsibility of all else upon the host and furnish only the reproductive organs for their own perpetuation. They serve that purpose effectively, however, although they are rootless, stemless, branchless and leafless plants. And yet they are no more lacking in vitality than are the most vigorous members of the vegetable kingdom.

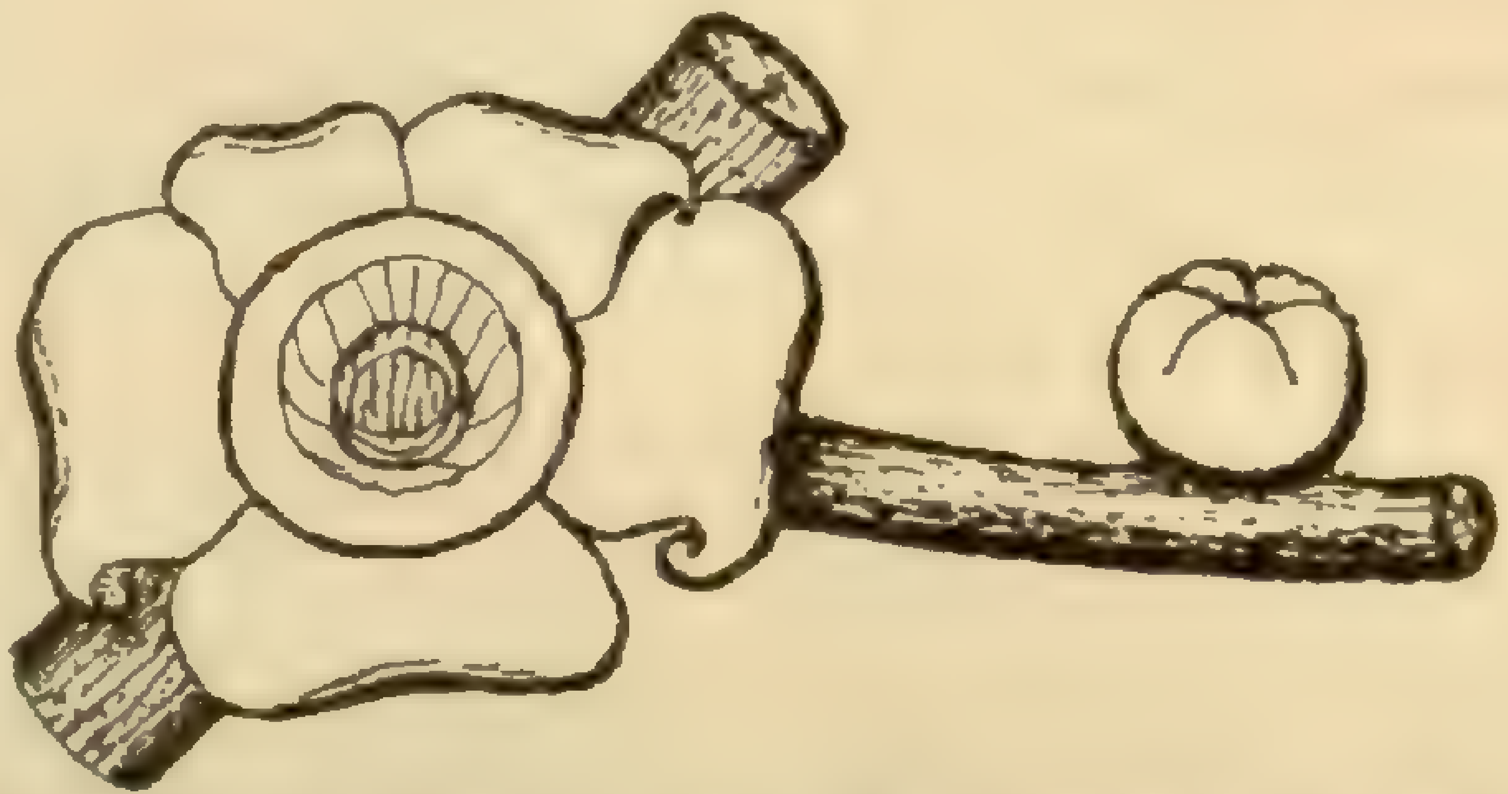

FIG. 8. Pen-sketch of *Rafflesia padma*, together with an undeveloped bud; sessile upon a branch of its tree-host. This species attains a diameter of eighteen inches when fully expanded in flower; but that is only half the diameter of the largest species of *Rafflesia*.

Although the seeds of Rafflesia, like those of the mistletoes, germinate upon the bark of a woody host, their embryo is not of normal structure, as is that of the mistletoes, but is simple and filiform, as is that of groups IV, V, and VII. Because the embryo of Rafflesia is not differentiated, and therefore has not a true radicle; and because it is not able to germinate upon the ground, it is assumed that the protruding end of its offshoot does not represent

the radicle of a normal embryo. If this assumption is correct it follows that the plant is destitute of normal epitropism and that the force with which the offshoot of the embryo pierces the bark and growing wood of the host is an abnormal and violent form of epitropism. It is also assumed that because the embryo of Rafflesia has no plumule the flower does not represent primary apotropism for the plant, but abnormal secondary apotropism as does that of the broom-rapes. The remarkable plants which constitute group VI are divided into many well-defined species and a considerable number of genera. Some of them bear the largest flowers that are known among plants, the largest being more than three feet in diameter, but some are very small. All are natives of warm climates, mostly of Asia, Africa and the adjacent islands. A few American species are known, all of them small. One very small species which is found in Texas and Mexico is sessile in great numbers upon a papilionaceous shrub, and is hardly more than one eighth of an inch in diameter when in full bloom.

GROUP VII

Group VII consists of a remarkable and varied series of tropical and subtropical phenogamous parasites known as the Balanophoreæ. Some of them have large and showy flowers, and some of them have so great resemblance to fungi that the older botanists regarded them as such. All of them are parasitic upon roots of woody hosts, beneath soil which is usually rich in vegetable mold. The seeds germinate upon the ground. The embryo is not differentiated into cotyledons, radicle and plumule, but it is filiform as is that of groups IV, V and VI, and its offshoot penetrates the ground in a manner similar to that of the broom-rapes. In the manner of their germination and in the underground origin of their flowering stems from a tuberous or amorphous mass, these plants also resemble the broom rapes; but in their florescence and fruitage they are very different. They produce no chlorophyl and they are all without either true roots or functional leaves.

although some of them have moderately large, scaly representatives of leaves.

There are probably other forms of phenogamous parasitism, but the seven fore-mentioned groups are the best

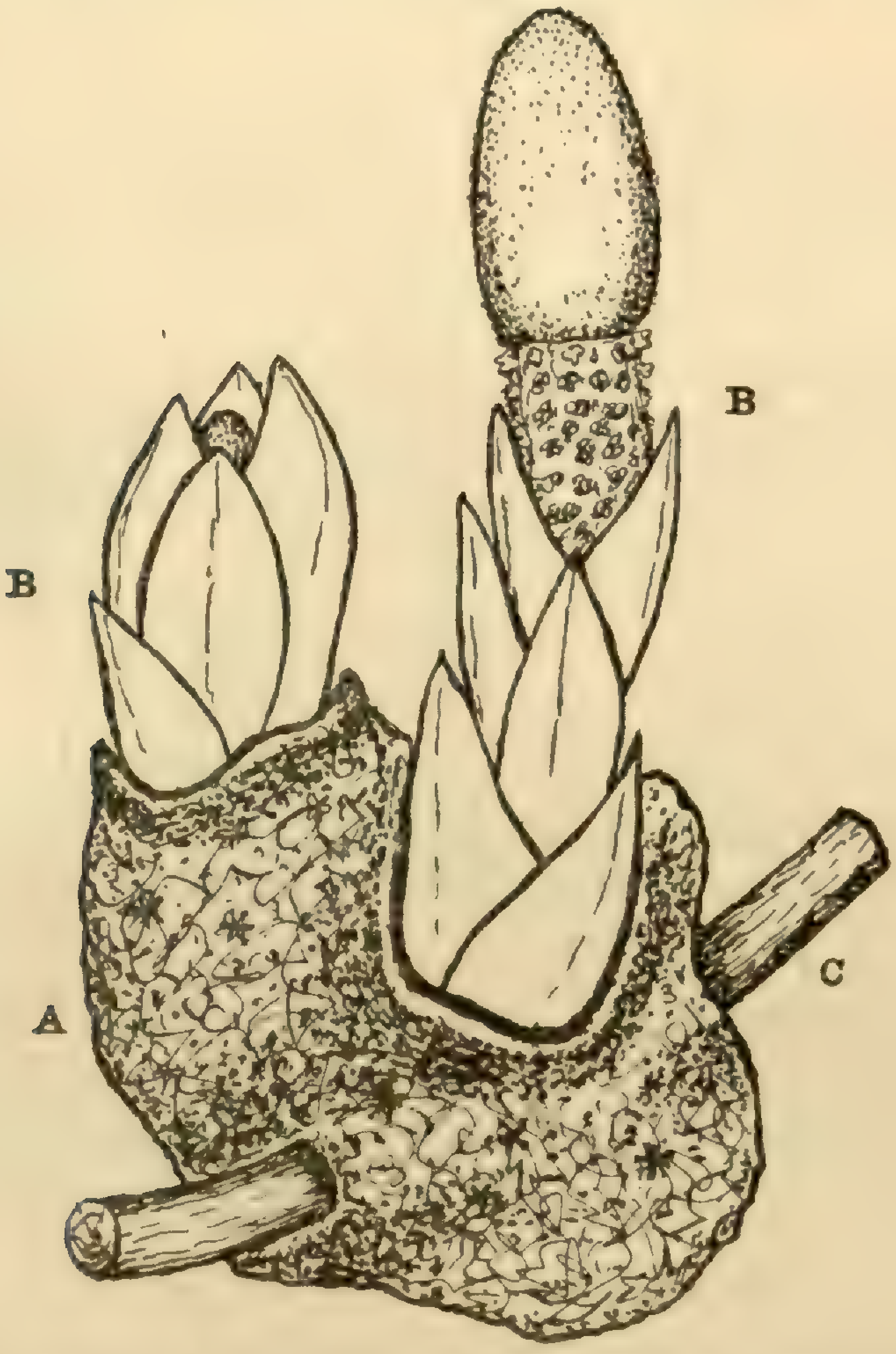

FIG. 9. Pen-sketch of *Balanophora hildenbrandtii*, a native of the Comoro Islands, off the east coast of Africa. After Kerner. One quarter natural size. The leaves of this species, although large, are scaly and not functional.

A. Amorphous, fleshy mass. *B, B*. Flower stems springing from the mass. *C*. The root-host.

known, and they serve to show that they are all depraved members of the class phenogams, and not predatory members of a separate class.

PRELIMINARY REPORT ON AN INVESTIGATION OF THE SEASONAL CHANGES OF COLOR IN BIRDS

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New York Zoological Park

It is a well-known fact that the males of many species of birds assume a special nuptial plumage at the beginning of the breeding season, sometimes radically different from the plumage of the winter. Especially marked examples are scarlet tanagers (*Piranga erythromelas*), bobolinks (*Dolichonyx oryzivorus*), and certain weaver birds of the genera Vidua and Pyromelana.

We know that the native birds mentioned above lose their brilliant breeding plumage in the early fall and assume a winter dress approximating that of the female. When we consider such a case as the scarlet tanager and the summer tanager (*Piranga rubra rubra*), the former changing annually from scarlet to green, the latter remaining scarlet at all seasons, we have an interesting difference in two closely related species giving definite data from which to work. The problem which I have set myself, and at the solution of which I have made but the merest beginning, is, What is the cause of, or what factors determine, this seasonal change in the males of the scarlet tanager and the bobolink?

So unbroken is the field of research in all such problems as this that the most hopeful way of working is to clear the ground by gradually eliminating all negative factors, and thus narrowing down to the important dynamic qualities of the environment.

On hastily reviewing the field, the following factors have occurred to me as being the most important in bringing about, either directly ontogenetically, or indirectly phylogenetically, seasonal change of color:

General condition of the bird's body—whether fat or thin.

Food—whether vegetable or animal.

Blood pressure—whether raised or lowered.

Sexual organs—whether active or inactive.

Inheritance.

Temperature—heat or cold.

Conditions of humidity or aridity.

This list is of course merely tentative, and the factors enumerated are by no means equal, and some are dependent on others. But they represent what I selected when first I began the experiment detailed below, as a convenient review of the field before me.

This experiment concerns only factor number one, the condition of fatness or thinness of the bird's body and its influence on moult and indirectly on the sequence of annual changes of color.

We know that birds, such as bobolinks and tanagers, after the cares of the breeding season are always thin and in poor condition. The externally worn and bedraggled condition of the feathers is reflected in the physically deeper part of the body, and the keel of the breast-bone—that true index of a bird's condition—often is very conspicuous under the skin of the breast. Not until the fall moult is past do the birds improve much in condition and then they become unusually fat. I think that these few facts hold true of most birds.

Fat is something to guard against in captive birds, and in the Zoological Park I find it necessary to have a weekly examination made of many of the small birds; this being a matter of regular routine. Birds from the various cages are caught and carefully examined, and the proportions of the food ingredients—fat-producing and the opposite—are regulated according to the condition of the birds.

One year ago last summer I took full-plumaged specimens of male scarlet tanagers and bobolinks in full song and plumage and put them under careful observation.

None of these birds had been allowed to breed, and so, although it was rather late in the year, they were still in the height of vocal and physical condition. They were all tame, and although during the period of experimentation they were confined in rather small cages, each bird in a space 12 x 12 x 24 inches, yet their plumage remained in almost perfect condition.

I began gradually to cut off the supply of light and slightly to increase the amount of food. This caused a corresponding decrease in activity of the birds, and an almost immediate increase of weight. The danger of obesity in caged birds is that any excitement or sudden fright may cause a blood vessel to break, or in some other way bring about death from apoplexy. Consequently I kept the tanagers in a room where they were never disturbed and where no noise ever made possible the chance of an untimely end.

A month later when the time for the fall moult arrived, the birds were living "the simple life" in a dim illumination and, although consuming a normal amount of food, were exercising but little. The time for the fall moult came and passed and not a single feather was shed. The cages were made of mosquito-netting wire and would have confined any moulted feathers. In addition to this, the birds were examined every third day, and nowhere on the body was there any sign of moulted or of new, incoming feathers. On blowing away the plumage from the breast, the yellow sub-cutaneous layer of fat could be distinctly seen.

In brief, the birds skipped the fall moult entirely and appeared to suffer no inconvenience whatever as a result. As far as appearance went they were in perfect health, showing only the symptoms of inactivity produced by an excess of adipose tissue. Early in the experiment the songs of the birds diminished and finally died away altogether, and when a good layer of fat had been acquired the birds seldom uttered even a chirp.

From time to time a bird was gradually brought into

the light for a week or two and meal-worms were added to its diet. This invariably resulted in a full resumption of song. Even in the middle of winter a tanager or a bobolink would make the room ring with its spring notes and with this phenomenon was correlated a slight decrease in weight. This phase of the experiment could not be repeated indefinitely, however, for the song period seemed limited, just as it is under normal conditions, although the nuptial plumage remained unchanged throughout the winter. As one of my keepers pithily put it, "We have their calendar twisted backward."

I found that a sudden alteration in temperature—either lower or higher—wrought a radical change in the physical metabolism of the birds. They would stop feeding almost altogether, and one tanager lost weight rapidly. A few feathers on the neck fell out, and in the course of some two weeks this bird moulted almost every feather and came strongly into his normal winter plumage of olive green. The metabolism set up by the change in temperature, in its extent and rapidity, seems comparable only to the growth of a deer's antlers.

Early in the following spring individual tanagers and bobolinks were gradually brought under normal conditions and activities, with quick result: just as the wild birds in their winter haunts in South America were at that time shedding their winter garb and assuming the more brilliant hues of summer, so the birds under my observation also moulted into the colors appropriate to the season. The old scarlet and black feathers fell from the tanagers and were replaced by others of the same color; from buff, cream and black, the bobolinks moulted into buff, cream and black! There was no exception; the moult was from nuptial to nuptial; not from nuptial to winter plumage. The dull colors of the winter season had been skipped.

I think we thus have proof that the sequence of plumage in these birds is not in any way predestined through inheritance bringing about an unchangeable suc-

cession, in the case of the tanager, of scarlet—green, scarlet—green, year after year, but that it may be interrupted by certain external factors in the environmental complex.

The further significance of these results I leave to others, or until I have more complete data, checked by results derived from control of the other factors of the environment. It would be worse than useless to formulate any theories at the present incomplete stage of the experiments.

The scarlet tanager is of especial interest, as I have said, on account of the absence of such an annual change of color in its near relative, the summer tanager, and experiments with the latter species may shed some light on the subject. Other experiments concerning half and even quarter moults are yielding interesting results and will soon be reported upon.

There is a great satisfaction in thus making even the merest beginning at threshing out these problems, which in their general evolutionary aspect are of far wider application than in the Class Aves alone. And work along these lines is all the more enjoyable because it entails the loss of no life as concerns the birds themselves.

NOTES ON THE BREEDING HABITS OF THE SWAMP CRICKET FROG, CHOROPHILUS TRISERIATUS Wied.

A. H. WRIGHT AND A. A. ALLEN

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About nineteen years ago, Professor O. F. Hay [1] while searching the ponds about Irvington, Indiana, for Ambystomas and their eggs discovered the eggs of *Chorophilus triseriatus.* The eggs were well advanced in development and his observations on the succeeding stages constitute most of what we know of the life-history of the swamp cricket frog.

While on a similar search for *Ambystoma jeffersonianum* in the suburbs of Buffalo one of us found several males and females of Chorophilus and, subsequently, some anuran eggs which for a time remained unidentified. Inasmuch as the identification of these eggs furnished data upon the mating, egg-laying process and fresh eggs of *Chorophilus triseriatus*—the period preceding that of which Professor Hay's observations treat—it seems advisable to present this material.

During the last weeks of March Chorophilus appears in considerable numbers about the outskirts of Buffalo. The male chorus which is easily distinguished from that of *Hyla pickeringii* rises from most of the swamps and temporary ponds, even within the city. The singers themselves, however, are not easily seen, for, upon approach, they become silent and further disturbance causes them to disappear into the vegetation at the bottom of the pond where they remain until some time after the disturbance has ceased. Then, from the most remote corner the chorus is gradually taken up until the whole pond resounds with the ringing notes. In taking up the

[1] Hay, O. P. Notes on the Life History of *Chorophilus triseriatus.* Am. Nat., 23 September, 1899, No. 273, p. 770.

chorus, the assurance evidenced by the single voice is extremely contagious. This fact makes it possible to overcome some of the difficulties which ordinarily present themselves in collecting this species. One has but to place the first captures in a bag or other close receptacle and carry it on one's person. The prisoners chirp up and sing as boldly as though undisturbed in their natural haunt. Their voices elicit an almost immediate response from those in the pond. Indeed, at such a time, with a little practise one can wade about, while they sing on all sides and dip up as many as one desires.

In this way after spending several hours in capturing the first two, 30 specimens, 25 males and 5 females, were taken in less than an hour. These were isolated for the purpose of studying the egg-laying process. On the way from Buffalo to Ithaca (April 1, 1907), they were kept in the same box, but the sexes in separate compartments. During the transit, the males chirped considerably and the females deposited 200 or 300 eggs without attendant males.

The Embrace.—The usual Hyla type of embrace obtains, the forearms of the male being pressed into the axillæ of the female. The males at the height of the breeding period evince an ardor almost as eager as that of the common toad. Sometimes, they embrace each other and as many as 4 or 5 males have been found in one bunch.

A peculiar embrace recorded June 16, 1907, may serve to illustrate how long this nuptial impulse may remain with the male. April 1, 1907, about 30 *Hyla pickeringii*, 1 female, 29 males, and 5 male *Chorophilus triseriatus* were placed in one jar. Between April 1 and June 16, these swamp cricket frogs ate nothing, yet, after 2½ months, and, evidently long past the breeding time, an emaciated male *Chorophilus triseriatus* mated with the single female *Hyla pickeringii*. The embrace was axillary, but sometimes, possibly due to weakened condition, the male partially lost his hold. Then, his arms slipped along on the sides of the body of the female until he came to the lumbar embrace, the arms touching each other on the ventral side. The male disliking this embrace sought

to move along the body of the female to the customary amplexation of his species. A similar weakened condition may explain the occasional records of lumbar embraces with other captive anurans which normally adhere to the axillary type.

At the height of the breeding season the male Chorophilus, like other Anura, often grasp moving objects or animals which are in the same aquarium with them.

The Egg-laying.—On the morning of April 2, 1907, the 25 male *Chorophilus triseriatus* were placed with the five females. At 9:50 A. M., the first mated pair was recorded and, within 20 minutes the female began laying. With one exception, she chose a different perch for each egg-laying period, thus giving a bunch to each period of sexual activity. In one instance she sought the same perch 3 successive times. She ordinarily grasped the branch with her forelimbs. When about to deposit she brought one heel up to the stem and near the vent. Farther back the other foot held the stem with the toes. Each time, just before the voidance of eggs the female raised her anus and the male stretched to bring his vent near that of the female.

This pair consumed 2½ hours in laying a complement of 500 or 600 eggs. The process required about 90 fertilizations and emissions. The intervals between a simultaneous fertilization and emission and a similar succeeding period ranged from 16–35 seconds, the common range 17–30 seconds, the modal time, 20 seconds, the average, 21 seconds. Each time, from 2–10 eggs were voided, being emitted in small strings, a condition which could be most readily seen when occasionally the eggs were unattached to the stem and hung down from the vent of the female. In such cases the strings broke after 10–12 eggs were voided. There were 16 periods of egg-laying, 20–70 eggs being usually laid at a period and each period consumed from 2–7 minutes, 3 minutes being the modal time. Always after a period of laying the pair arose to the surface of the water. These 15 periods of rest varied

from 2–17 minutes, the mode being 4 minutes. All the eggs were laid in water 66° F.

An account of the first pair follows in tabular form:

Number of Sexual Periods.	Length of Sexual Activity.	Intervals Between Periods of Sexual Activity.	Number of Eggs.	Fertilizations and Emissions.	Intervals between Each Emission.
1	3 min	17 min.		8	
2	7 "	4½ "		7	
3	3½ "	5 "	2–7	8	
4	3 "	11 "		9	20, 25, 20, 17, 22, 17, 20, 21 secs.
5	5 "	2 "		14	20, 18, 17, 20, 22, 20, 20, 20 "
6	2 "	2 "		4	18, 20, 18 "
7	3 "	4 "		7	35, 17, 20, 25, 23, 18 "
8	3 "	3 "		6	22, 23, 25, 20, 18 "
9	2 "	16 "		7	20, 20, 22, 17, 17, 17 "
10	4 "	3 "		9	28, 27, 27, 22, 22, 20, 23, 17 "
11	4 "	4 "	2, 2, 3, 3, 7, 4	6	
12	2½ "	10 "		7	
13		6 "	3	1	
14		5 "	2	1	
15		15 "	2	1	
16	1½ "		2, 8, 4	3	

The Eggs.—The second pair were in the embrace at noon. At 1:30 P. M. they began laying and by 4:30 P. M. their complement numbering 600 eggs was laid. The complements of females of *Chorophilus triseriatus* vary from 500–800 eggs. The mature eggs of one ripe female, 3.2 cm. long, numbered 418 for the right ovary, 354 for the left, or a total of 772.

The eggs are laid in bunches and are attached to twigs, branches, fine roots or grass stems. Each bunch contains from 30–100 eggs. An actual count of 5 bunches gave 50, 80, 70, 68, 70, respectively.

The measurements of eggs gave the following results: the average vitellus diameter of 38 eggs was 1.1 mm., the mode, 1.2 mm., the range, .9–1.2 mm.; the average envelop diameter was 5.8 mm., the mode, 5.6 mm., the range usually 5.0–7.8 mm., though sometimes as low as 3.0 mm.

The vegetative pole is white; the animal, brown or black. The envelop about each individual egg makes up the larger portion of the jelly mass of a bunch, yet, there is in addition, some connecting jelly. This has a loose gelatinous consistency and does not envelop the whole mass as in Ambystoma.

MODERN METHODS OF EXCAVATING, PREPARING AND MOUNTING FOSSIL SKELETONS

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The work of collecting and preparing fossil bones is so well known in the museums of America that it is not my intention to explain in detail how to take up bones in the field and to prepare them in the laboratory. Some of the most modern methods adopted in the American Museum of Natural History may, however, be of interest.

FIELD WORK

Too much emphasis can hardly be laid upon the proper treatment of bones in the field, because very crumbly but precious specimens may be saved by proper treatment, while, on the other hand, good specimens may be ruined by wrong treatment.

Up to recent years collectors in the field have used almost exclusively gum arabic for saturating soft bones in order to harden them, and while practical for very porous bones it does not penetrate sufficiently into less porous ones, so that they become hardened on the outside only, remaining crumbly inside. Another disadvantage is that gum will absorb moisture and loses its binding properties in damp weather. Shellac will penetrate the bones much more thoroughly than gum, and when sufficiently dry will leave them much harder and absolutely waterproof. For the last three or four seasons our collectors have used a solution of shellac in place of gum arabic with very good results; and this can be recommended for any field work wherever the fossils are porous and badly preserved. Brown shellac is better as it dissolves more easily and it is stronger, and should be used

wherever practicable, but for light-colored bones white shellac is preferable, as it will not discolor the bones.

Preparing Bones in the Laboratory

Bones treated in the field with a solution of shellac usually arrive in the laboratory in better preservation than those treated with gum or glue-water, and much less care is necessary to prevent wetting in freeing them from the matrix or burlap cover. Numerous methods are employed to remove the matrix from the bones, according to the condition of the specimens. While a good-sized chisel is practical on a large and well-preserved specimen, small and delicate bones may be freed more securely with so-called harness awls of different sizes, bent and hardened to suit as a gouge and as a scratcher for softer matrix. Wherever the system of pneumatic chisels can be introduced it may be of great importance, especially for lighter chiseling of not too hard rock; it works very rapidly and with less injury to the specimens, as I had opportunity to observe in the Field Museum of Natural History at Chicago.

I have found in my experience that a moderately strong solution of gum arabic used with alabaster plaster is a good and very practicable cement with which to fasten pieces together and is the best cement for all ordinary bones. When used in the right proportions it holds very well, at least as well as the expensive cements, so much advertised. I find that the best and most substantial plaster for restoration work is made by mixing the plaster in a solution of yellow dextrine which can be easily dissolved in boiling water. The dextrine solution should not be too strong; the right strength is indicated when the solution is of a light coffee color. Too much dextrine causes the plaster to crack when dry.

So-called plasterine or modelling clay furnishes a very good material for moulds for rough casting. In this work the bones are slightly coated with glycerine and pressed in both halves of the clay mould in such a way that they

can be lifted out without changing the shape of the mould. The two halves are then placed together properly and filled with plaster, which makes a fairly accurate cast. In many cases I have made the casts larger than the objects by moving the specimen to and fro in the mould to enlarge the cavity. When modelling missing bones much time is saved by casting a bone in this manner and then modifying the form to suit, with knife and awl, instead of modelling the missing bones in clay.

Mounting of Skeletons

The mounting of fossil skeletons is a problem which can not be explained in a general way. Every skeleton has to be treated according to its size, shape, and condition. Skeletons from the size of a cat up to that of a large dog, to be mounted free, can be supported with light soft steel, so that the mounting shows very little. In case the vertebræ are not to be made detachable for study purposes, a flat rod may be run through the neural canal, which makes the neatest mount.

Limbs and ribs supported with flat soft steel, fitted close to the bones, look very well and the mounting is very inconspicuous. All soft bones may be bored and fastened to the supports by screws or pins; harder bones by means of very small flat bands, fitted around the bones and fastened on the main supports with pins or screws.

I may mention another method which I have introduced in the American Museum that may prove to be valuable for other museums. Skeletons which are soft enough, so that the bones can be bored, can be mounted so that every bone is easily detached in the following manner: The back-bone may be supported by a soft steel rod (flat or half round) running under the vertebral column. Fittings to slide over the rod can be cast in bronze without great expense. Each fitting has a pin fastened to it which runs into the centrum of the vertebra, holding it firmly. Pins made stationary by being fastened in the supporting rod do not answer as in many cases it is impossible to get

the individual vertebræ in or out of the column without moving the adjacent vertebræ and pins. After the limbs have been temporarily set up and the flat or half round steel fitted flush to the bones, holes may be bored in the supports and in the bones at the proper places and brass tubes inserted and fastened in the bones with a mixture of shellac and whitening, which holds them very firm. Before the tubes are inserted a thread should be cut inside the tube to which the supports can be screwed very securely. This makes the bones easily detachable. This method is desirable for all skeletons with soft bones, small or large, and especially large skeletons, such as the Mammoth or Mastodon, can be mounted with comparatively few rods or uprights. I can not recommend any style of iron or steel for all purposes as that largely is a matter of individual taste. I myself prefer half round, soft iron for all large skeletons to be fitted along the bones. For very small skeletons, small flat steel is preferable. The so-called channel iron makes good rib supports for all larger skeletons, as there is in the channel a suitable place for the nuts of the screws.

A very practical tool to use in mounting skeletons, especially larger ones, is the "electric drill." It can be attached to any electric light block, and is a great labor-saving tool, which I can recommend very highly. We have one in use in our laboratory which weighs eight pounds; it cuts a ¼-inch hole, can be handled very easily, and can be used to drill holes in any bone or iron without taking them out of place.

Another new feature of importance is the over-head rail or trolley system. As installed in our laboratory, a comparatively heavy rail is fastened to the ceiling, on which trolleys with hoisting blocks attached can be rolled very freely to and fro. Skeletons suspended by these blocks can easily be raised or lowered, or moved from one end of the room to the other. This system is of great importance for economy in mounting very large skeletons. To suspend small skeletons while in operation we use

steel rods screwed to tripods of different sizes for uprights with a horizontal bar fastened by means of clamps, which allow it to be moved up and down. This is a simple apparatus and is very useful for suspending skeletons of not too large dimensions.

To dispense with most of the plumbers' fittings in mounting skeletons we have introduced during the past few years a mode of splitting steel at the end, to act as braces and in other ways, opened and flattened and screwed to the uprights and other supports. This perhaps takes a little more time than to use so-called plumbers' fittings, but it appears as an entirely different style of mounting.

Wherever electric power is available labor-saving machines can be installed, such as drilling machines for heavy work, rotary saws for splitting and cutting steel and brass, small turning lathe attachment for corborundum wheels, and rotary diamond saws for large section cutting. All these appliances just mentioned we have attached to one large lathe run by a one-horse power motor, although a little stronger motor may be recommended. A small gas-blast furnace with a one third or one half horse power motor for the blower makes a sufficiently strong forge to heat a two-inch steel bar and we find this in our laboratory indispensable.

During later years we have introduced numerous other convenient tools, but it would take too long to mention them all here.

ISOLATION AND SELECTION IN THE EVOLUTION OF SPECIES. THE NEED OF CLEAR DEFINITIONS

JOHN T. GULICK

THE discussion concerning the factors in organic evolution has been obscured by the diversity of meanings given to the same terms by different writers, and sometimes by the same writer. What do we mean by isolation, by selection, by environment, by evolution?

DIFFERENT MEANINGS GIVEN TO ISOLATION

I think that in Darwin's books isolation is always used to designate the prevention of free-crossing between different groups by means of factors lying outside of the groups, such as geographical barriers, but it has since been extended to mean the prevention of free-crossing by any means. Professor Kofoid, in his article in *Science* for March 29, 1907, gives the word this broader meaning in one place; but he must use it in a more limited way, when in the last sentence of his article, speaking of what DeVries finds in the elementary species "coincidently appearing" in the evening primrose, he says: "Isolation plays no part in their origin or continuance." I have not found any statement by DeVries maintaining that elementary species remain distinct forms from the original stock, when free-crossing with the original stock continues. In my volume on "Evolution, Racial and Habitudinal," pp. 5, 69–70, 155–156, I call attention to a mutation arising in certain species of snails, and probably producing complete isolation between the new form and the old, though both are occupying the same tree. The hermaphrodite snail is so constructed that it seems impossible for one of sinistral form to cross with one coiled in the opposite way; but in the Hawaiian Islands there are

a number of species presenting both forms. If direct crossing is impossible, it follows that the only chance for continued connection between the two forms is through the subsequent mutation of one or both of the forms; and we know that in some species this occurs in a small percentage of the offspring of each generation.

That isolation is not a necessary condition for the production of this mutation is shown by the fact that it rises suddenly in the midst of an intergenerating group; but the fact that it remains a distinct form, returning to the original form in only a small percentage of the offspring, seems to be due to the fact that by its structure it is prevented from crossing with the original stock. In other words, structural isolation, which is one form of autonomic isolation, produces racial demarcation and initial segregation, opening the way for intensive segregation, through the introduction of divergent forms of selection.

That natural selection is not the cause producing this mutation is shown by the fact that the old form and the new form are equally adapted to the same environment. I, however, maintain that the structural isolation produced by the mutation prepares the way for the introduction of permanently divergent forms of selection.

Different Forms of Selection

In the case of selection as in that of isolation, we find autonomic as well as heteronomic forms. Artificial selection as applied by man to the propagation of domestic plants and animals is a heteronomic factor; and in order to obtain permanently divergent races from the same stock, certain divergent variations or mutations are subjected to divergent forms of selection, while at the same time the different types are artificially isolated, unless there are autonomic factors holding the types apart. Such factors are preferential mating due to sexual and social instincts, or some degree of segregate fecundity; and in plants prepotence of pollen on the stigma of the same type, or flowering at different seasons. Natural selection is a form of heteronomic selection; for, as de-

scribed by Darwin, it is subject to change, only as the group is exposed to changed external conditions resulting in the survival and propagation of an average type differing more or less from the average birth type. Darwin also carefully described one form of autonomic selection, which he called sexual selection. In my volume on "Evolution, Racial and Habitudinal," I have called attention to social and filioparental selection, and several forms of impregnational selection, besides endonomic selection, in which the different methods of using the same environment, adopted by isolated branches of the same species, lead to the survival of different types of variation. These and other forms of autonomic selection must be considered in any complete analysis of the factors producing two or more divergent species from one original species.

Variation and Heredity and Their Control

If my analysis of the factors producing divergence is correct, the active cause is found in the powers of variation and heredity possessed by the intergenerating group, while the conditions controlling, shaping and molding the variation and heredity are those that are designated by the terms isolation and selection. Isolation produces demarcational segregation; and divergent forms of selection in the isolated groups will produce intensive segregation, if isolation at the same time continues to hold the groups apart.

Romanes describes selection as a form of isolation, because its influence in controlling variation and heredity is due to its preventing those that survive from crossing with those that perish before propagating. That the influence of both isolation and selection is due to the prevention of free-crossing is certainly true, and, as I have further pointed out, both classes of factors cooperate in producing segregation. It think, however, that it is in better accord with the meaning that writers on natural history have usually given to the two terms to define isolation as the prevention of free-crossing between groups of

organisms *existing at the same time.* In certain cases the isolative process may be selective at the same time; and so demarcational and intensive segregation progress together; as is seen when the strong and courageous migrate together, leaving the weak and timid in the old habitat.

Diversity in the Use of a Complex Environment

An illustration of the wide divergence that may take place in a single family distributed over a small area is found in the Achatinellidæ, a family of snails found only on the Hawaiian Islands. Some genera of this family are found only on the ground, others chiefly on the trunks and branches of the trees, others on the leaves of the trees and shrubs. Ages of divergent evolution have made the individuals of each genus entirely incapable of crossing with those of other genera; but in the case of closely related varieties and species occupying different species of trees in the same valley the conditions are very different. These are cases in which the continued isolation can not be attributed either to external barriers or to physiological incompatibilities. The different methods of using the environment, whether due to habits or to inherited characters, is the real cause of the isolation. Again, of the ten genera of this family some are confined to one or two islands, though the vegetation and other conditions surrounding the family are much the same on the seven islands of the group. The condition explaining the small area occupied by any one of the five hundred species of this family is the limited power and opportunity for migration or transportation; and the great variety of types presented is undoubtedly due, first, to the power of variation possessed by isolated branches of the same species while using like environments in the same way; and second, to the variation in isolated groups introducing divergent methods of using the same complex environment and so subjecting themselves to divergent forms of selection, even when no external barriers hold them apart.

In *Science* for March 30, 1906, Dr. Ortmann refers to species of crawfish subjecting themselves to diverse con-

ditions, in isolated positions, by diversity in their "ecological habits." He describes them as "cases of ecological (or binomic) isolation, where no 'barriers' in the ordinary sense are present." In the relations of Hawaiian snails such cases are not infrequent. Even when the conditions in the environment with which the organism deals are extremely simple, the divergent groups of the original stock may adopt several different methods of dealing with these conditions, and with marked success in the use of each method. A fine illustration of this fact is found in the different species of Triposolenia, a genus of pelagic protozoa described by Professor C. A. Kofoid, in the University of California Publications, Zoology, Vol. 3, Nos. 6, 7 and 8, December 11, 1906. After considering the nature of the several different types found coexisting in the same region, "in the surface waters of the sea," he concludes that, "The utility of each of the complexes of characters is sufficient for their preservation without the necessity of calling in *natural selection* to account for their differentiation and continuance." (See pp. 121, 123.)

Causes of the Earlier Forms of Divergence

In the discussion that has appeared in *Science* during the past two years, the chief interest has centered around the question of the causes of the earliest forms of divergence. One method of inquiry has been to observe whether in a given family of organisms the most nearly allied species and races are found in the same or in separate districts. If with great uniformity the nearest allies are found in separate districts, there is good reason to believe that initial demarcation has been due to geographical barriers, or at least to local isolation. If the analysis already given is correct, the first step in divergence must be sought either in some process of migration, or transportation producing local isolation; or in some variation in form, or habits of feeding, or instincts for mating, or time of flowering, or in prepotence of pollen, or in some other quality producing incompatibilities, and so producing

autonomic isolation. In such creatures as snails, it would seem that the different forms of impregnational isolation do not often arise before a considerable degree of divergence has been reached; for usually the most nearly related races, or varieties of Achatinella are found on separate groves of the same species of trees, in different parts of the same valley; while the most closely related groups of varieties, that are classed as separate species, are usually found in separate valleys; though sometimes in the same valley, but living on different species of trees.

In the case of plants, I have seen closely related species growing beside each other, and in some such cases they are found to flower at different months of the year, and in other cases it would probably be found that they are held apart by the prepotence of pollen of a given species on stigmas of the same species. In some of these cases where the present form of isolation is undoubtedly autonomic, it may be impossible to say whether the new type was not first developed in a few individuals, that for a generation or two were partially isolated geographically or locally in some sheltered nook.

Do New Types Continue in Spite of Free-Crossing?

As we have already shown in certain species of Hawaiian snails, a sudden mutation may arise, which by its very constitution is prevented from crossing with the parent stock; and in such cases it is evident that a permanent type may begin with the mutation. But is there any proof that a mutation that freely crosses with the original stock will remain unchanged, each type thriving and remaining unblended with the other? If the mutation is the dominant form, it may be granted that it will in time overwhelm the original form; but can two closely related races or species freely cross with each other, for many generations, without either type being affected by the process? For an answer to this question I would refer the reader to an article by Robert Greenleaf Leavitt in The American Naturalist for April, 1907. On pp. 214–217 he gives quotations from Professors Davenport,

Castle and Forbes, showing that "Everywhere unit characters are changed by hybridizing." This testimony is chiefly from those who have experimented with the crossing of animal forms, but even in the case of plants, there is reason to believe that when free-crossing continues divergence is checked. There is reason to believe that even with plants the controlling factor in each case of continuously divergent evolution is either some form of heteronomic isolation or some form of variation introducing autonomic isolation.

Moritz Wagner's Theory and My Theory were Isolated and Divergent from the Beginning

Moritz Wagner, in his "Law of the Migration of Organisms," was the first to insist on the importance of geographical isolation as a factor in evolution, but when he asserted that without geographical isolation natural selection could have no effect in producing new species he went beyond what could be sustained by facts. My own theory, though it did not take form till four years later, was reached without any knowledge of his, and therefore in complete isolation from his; and when they came together for comparison they were found to be quite divergent.

In March, 1868, Moritz Wagner read a paper before the Royal Academy of Sciences at Munich on "The Law of the Migration of Organisms," and in 1873 an English translation of a fuller paper by him entitled "The Darwinian Theory and the Law of the Migration of Organisms" was published by Edward Stanford, of London. It was through this pamphlet that I became acquainted with his theory concerning the impossibility of the production of new species except when and where migration establishes a colony geographically isolated from the original stock. In this paper we read: "The constant tendency of individuals to wander from the station of their species is absolutely necessary for the formation of races and species" (p. 4). "Where there is no migration, that is, where no isolated colony is founded, natural

selection can not take place" (p. 59). These and many other passages of similar import indicate how fully he recognized the importance of isolation, and how at the same time his theory was a denial of some of the facts in the origin of species. The following are some of the facts with which his general theory as well as his special statements were in conflict:

1. That, through change of climate and of other conditions due to geological changes, the whole fauna and flora of an island like Iceland might be subjected to new forms of selection producing a complete change of many species into new species, without any chance for migration. After the publication of my article in *Nature*, July 18, 1872, in which I emphasized the importance of isolation, I met Darwin at his home, and he called my attention to Wagner's theory, and suggested that it did not correspond with the facts of nature, especially on this point.

2. That the influence of geographical isolation in producing divergence, and in opening the way for selection to cooperate in producing divergence, is wholly due to its prevention of free-crossing, and that the same result may, in various ways, be brought about by divergent habits or instincts, or other incompatibilities, while the isolated groups remain in the original habitat of the species.

3. That divergence does not necessarily require the influence of different forms of selection.

4. And that different forms of selection do not necessarily depend on exposure to unlike environments; for diversity in the forms of selection may be due to diversity in the methods of using the same environment adopted by isolated branches of the same species.

In August, 1872, I read before the British Association for the Advancement of Science a paper on "Diversity of Evolution under One Set of External Conditions,"[1] in which the conditions just mentioned were briefly stated. In two subsequent papers entitled "Divergent Evolution through Cumulative Segregation," and "Intensive Seg-

[1] This paper was soon after published in the Linnean Society's *Journal*, Zoology, vol. XI, pp. 496–505.

regation,'' read before the Linnean Society in 1887 and 1889, and published in their *Journal*, the subject was more fully discussed, and since then in my volume on ''Evolution, Racial and Habitudinal,'' published by the Carnegie Institution, my view of the factors of organic evolution has been presented, with special relation to their interaction on each other, and the close correlation between the evolution of habits and the evolution of racial characters. It is to this last-mentioned phase of the subject that I have hoped that I might call special attention. I regard this influence of acquired habits in the control of the forms of selection as of great importance, especially in the evolution of the higher classes of animals, and in the races of mankind.

Meaning of the Term Environment

In all my discussions, I have been careful to give a uniform meaning to the term environment. When treating the evolution of species, or of smaller groups of intergenerating organisms, the environment is, in my language, always the set of influences lying outside of the group under discussion, and is never used to designate the influence of one part of the group upon another part, as, for example, the influence of parents upon offspring, of males upon females, of the strong upon the weak. In the generalizations made by some writers, it is impossible to decide whether the environments referred to are intended to include these reflexive influences or not. But even with the broadest interpretation of the term environment, I can not accept the statement often made that there is no divergence in branches of the same species unless they are exposed to different environments.

Such a conclusion seems to be based on the assumption that all transformation in organisms is due to adaptations giving more or less advantage to the forms that survive, and ignores the fact that in many species there are countless variations of a non-utilitarian character. It also fails to recognize the fact that isolated groups of individuals of the same variety, exposed to the same external

environment, and also to the same internal influences producing selection, may still, before many generations have passed, adopt different methods of dealing with the external environment, or introduce divergent forms of sexual or social selection, or of some other form of reflexive selection. The divergence, in such cases, is explained by the power of the species to vary, and by the probability that the variation will introduce new methods of meeting surrounding conditions. F. W. Headley, in his volume on "Problems of Evolution" (on pp. 146–149), gives illustrations of how branches of the same species may adopt *"alternative methods of adjustment to the same environment,"* and yet in the same book (on p. 103) we read: "If the environment remains unchanged, evolution ceases," and on p. 153—"Nothing but change of environment can lead to further evolution." His mind seems to cling to the old statements of general laws, though he has come to recognize a class of facts that are quite at variance with these old statements.

It therefore appears that we need not only a clear and consistent use of terms, but a clear and consistent statement of the facts of the organic world, in their bearing upon the changes that take place in organisms. I have carefully studied O. F. Cook's article in *Science* of March 30, 1906, and his previous papers to which he refers in that article. The chief difference in our estimates of the factors of evolution seems to me to result from a difference in the meanings that we give to the word evolution. In my use of the word all changes and divergences in the inherited and acquired characters of organisms are included. The chief factors I find to be variation and heredity in an intergenerating group moulded and controlled by isolation and selection. Fuller statements will be found in my book on "Evolution, Racial and Habitudinal," pp. 60, 79–80, and 138. Of these factors Dr. Cook says that variation and intergeneration relate to evolution, but isolation and selection, though "factors of species-formation, are not at all factors of evolution." It is evident that this difference in our enumeration of the factors of evolution is due to the different meanings that we give to the term evolution.

NOTES AND LITERATURE

EVOLUTION AND HEREDITY

Darwinism To-day.[1]—"Charles Darwin was the foremost scientific man of the entire nineteenth century, and I think he must also be termed the greatest Englishman of his time. Even the very few persons who would assign to the famous naturalist a less solitary preeminence must admit that his ability was of the highest order." Such an estimate of Darwin, recently expressed by Professor Minot, is seldom presented in discussions of *Darwinism.* Those using this term must explain that they do not mean the origin of coral islands through subsidence of the ocean floor, or the overturning of the earth by worms, or the adaptations of plants to cross-fertilization, or even organic evolution, but that they have in mind natural and sexual selection and perhaps also pangenesis. The recent book by Professor Kellogg is a discussion of the various theories of evolution.

The first chapter introduces the reader to the "philosophic turmoil and wordy strife," very little of which is said to have found its way into current American literature. In the second chapter it is stated that the "millions of kinds of animals and plants can have had an origin in some one of but three ways; they have come into existence spontaneously, they have been specially created by some supernatural power, or they have descended one from the other in many-branching series by gradual transformation. There is absolutely no scientific evidence for either of the first two ways; . . . If such a summary disposal of the theories of spontaneous generation and divine creation is too repugnant to my readers, . . . then my book and such readers had better immediately part company; we do not speak the same language."

There is little depth in such a statement. It will be generally conceded that existing animals have descended from the past,

[1] Kellogg, V. L. Darwinism To-day. A discussion of present-day scientific criticism of the Darwinian selection theories, together with a brief account of the principal other proposed auxiliary and alternative theories of species-forming. New York, Henry Holt and Company, 1907. 403 pp. $2.00.

and that at some remote time one or many forms first appeared upon the earth. Some will say that they appeared spontaneously and others that they were a divine creation, just as present occurrences are regarded by some as spontaneous and by others as divinely ordained. However, that the debate should not be checked by philosophy, the author hastens to consider the various attacks on "Darwinism," the defense, and finally other theories which may be substituted. His style is breezy, such as Englishmen describe as American, and New Englanders as Western.

"Sexual selection is one of Darwin's supporting theories which has nearly gone quite by the board." In support of this Mayer's convincing experiments with *Callosamia promethea* are fully described. "If there is any moth species in which the colors and general pattern of the male ought to be readily obvious to the female . . . it is this species." Mayer found that the females did not prefer normal males to those from which the wings had been clipped, or to those on which the red-brown wings of the female had been fastened in place of their own black ones of very different shape. The author believes that a satisfactory explanation of sexual dimorphism is yet to be formulated.

The importance of selection in producing mimicry in color patterns is accepted, though somewhat doubtfully. Professor Kellogg says of Basilarchia—"But thanks to its perfectly mimicking color-pattern, it wings its deceitful way unmolested. There is huge usefulness here, and selection can well be the steadfast maintainer of the viceroy's dissimulation." The marring of the resemblance by the dark streak across the hind wings is noted but not accounted for: the "over-refined" resemblance of Kallima to a leaf is called "absurd." The author leaves his reader to draw his own conclusions in regard to mimicry and many other problems. Thus Bumpus is cited to show that a storm destroys the physically defective sparrows, and Kellogg shows that a drought destroys the fit and the unfit fish. The reader must judge whether it is variation or "hard luck" which usually brings destruction.

Three theories alternative with selection are presented, namely, "Lamarckism," orthogenesis, and heterogenesis (mutation). Darwin is cited in favor of all three. Lamarck's conception of evolution is "a great thought and a clear one," but it lacks

experimental support. Likewise for the theory of heterogenesis as capable of explaining species formation as a whole, the author finds an "extreme meagerness in quantity of the real scientific evidence." He declares that no indubitable cases of species-forming or transforming have been observed.

"The theories of orthogenesis of the general type exemplified by Eimer's are directly in line with the spirit of modern biological methods and investigations. They rest on the assumption that physico-chemical factors produce direct effects on the plastic organism, and that such effects . . . modify or control evolution." Any tendency, such as is shown by Nägeli, to substitute a "mystic vital force" for the "physico-chemical factors" receives the author's severe censure; yet except as one emphasizes the complex and unknown internal factors rather than the simpler conditions of environment, these conceptions are not far apart. "Nägeli believes that animals and plants would have developed about as they have, even had no struggle for existence taken place, and the climatic and geologic conditions been quite different from what they actually have been." Much more could be said in favor of orthogenesis than Professor Kellogg records.

In the concluding chapter it is stated that "Darwinism, then, as the natural selection of the fit, the final arbiter in descent-control, stands unscathed, clear and high above the obscuring cloud of battle. . . . To my mind every theory of heterogenesis, of orthogenesis, or of modification by the transmission of acquired characters confesses itself ultimately subordinate to the natural selection theory." Yet before closing, Professor Kellogg returns to a discussion of orthogenesis as "a determinate though not purposeful change."

After each chapter there is an appendix containing considerable citations from works on evolution. The volume should prove valuable to students; we hope that they will not lay it aside with the author's remark "*Kurz und gut*, we are immensely unsettled."

F. T. L.

The Effect of Environment upon Animals.—It is well known that if the pupæ of certain butterflies, *e. g.*, Vanessa or Pyrameis, be subjected to extreme cold (0° to — 20° C.) many of the adults will be aberrant in color pattern. However, if they be subjected to extreme heat (42° to 46° C.) the same aberrations

will be produced. Less extreme heat (35° to 37° C.) gives aberrations differing from these. Opinions do not agree as to the reason why extreme heat and extreme cold produce the same results. M. von Linden considers it to be a "pathological" phenomenon caused by tissue injury. Narcotizing and whirling on a centrifugal machine cause similar effects. Fischer[1] argues with great force that this is not so. He believes it to be a "normal" arrest of development, such as occurs during hibernation, pointing out, however, the difficulty of drawing a sharp line between normal and pathological physiology. Both Vanessa and Pyrameis are common in America. It would be well worth while to study critically the inheritance of these abnormalities.

Salamandra maculosa is normally either viviparous or oviparous, producing a large number (up to 72), young. These young, when born, are larvæ. They live in water for some time, finally losing their gills and metamorphosing into land salamanders. If, however, the female be deprived of water, she will give birth to a small number (2 to 7) of young which have already lost their gills. Kammerer[2] carried the experiment still farther and found that, even if the abnormally born females be given water, they give birth to young having reduced gills.

Plate[3] has made a detailed study of the genus Cerion (land snails) of the Bahama Islands. Many local races or varieties were found. He believes these to be due to the modifying influence of the environment, but gives no experimental evidence. Snails could easily be transplanted from one island to another in order to test this point. The Bahama Islands are so near to America that this problem should appeal especially to American students of evolution.

FRANK E. LUTZ.

[1] Fischer, E. Zur Physiologie der Aberationen- und Varietaten-Bildung der Schmetterlinge. *Archiv für Rassen- und Gesellschafts-Biologie*, IV. 6, November–December, 1907.

[2] Kammerer, Paul. Die Nachkommen der spätgebornen *Salamandra maculosa* und der frühgebornen *Salamandra atra*. *Archiv für Entwicklungsmechanik der Organismen*, XXV, 1 and 2, December, 1907.

[3] Plate, C. Die Variabilität und die Artbildung nach dem Prinzip geographischer Formenketten bei den Cerion-Landschnecken der Bahama-Inseln. *Archiv für Rassen- und Gesellschafts-Biologie*, IV, 4 and 5, July–October, 1907.

THE PROTOZOA

Some Recent Protozoa Literature.—Waves of special enthusiasm sweep over the domain of biology as of other sciences; each leaves its mark, passes on and is followed by others. At one time it was the "section cutters" at another the "finger bowl brigade," at present it is genetics. Some investigators are independent enough to swim in quieter waters while some are so bold as to try to make an independent high-water mark long after the wave has passed. To the later group Hartmann and Prowazek must be assigned, for in a recent paper[1] they deal with the homologies of the centrosome, a problem which has never been solved and one that can not be regarded as obsolete, but which is no longer on the wave of biological enthusiasm.

Nor is the point of approach at all novel. They see in the nucleus and centrosome of the higher cell types only the reminiscence of a dual condition in protozoa. To be sure, they bring to bear a great fund of recently published observations, more particularly on protozoan cell structures, and they see in the metazoan nucleus and centrosome the outcome of dimorphic nuclei in these primitive animals. The two nuclei of the hypothetical ancestral form are not of the type suggested by Schaudinn in the early advocacy of this same theory (*Amœba binucleata*), but of the type seen in Trypanosoma, where trophonucleus and kinetonucleus are persistent morphological elements of the cell. They believe that the same dual arrangement is present in other protozoa; in some the kinetonucleus is reduced to a mere granule outside of the normal cell nucleus (as in the Centralkorn of the Heliozoa); in others the two nuclei are united to form an "amphinucleus," the one encased within the other as in the typical centronucleus. Here is the only really novel point in their discussion, and this can not be accepted, for to assign to the division center in a nucleus of the Euglena type the rôle of an independent nucleus is a *reductio ad absurdum*. The authors use a considerable area of printed matter to prove that these kinetoplasmic structures in protozoa are homologous with the centrosomes of higher forms, a point of view generally accepted more than a decade ago; and certainly nothing new is gained

[1] Hartmann and Prowazek. Blepharoplast, Karyosom und Centrosom. *Arch. f. Prot.*, X, 2–3.

by calling these division centers "nuclei." The one feature in support of this view is the presence of chromatoid material about the blepharoplast in Trypanosoma and in Paramœba, but even the truth of this is not generally accepted, Schaudinn's observations not having had sufficient confirmation to warrant universal acceptance. The authors' statement that chromatin material is likewise present in the great sphere of Noctiluca is not true. On the whole this conception of blepharoplast, karyosome and centrosome gives an inadequate summary of the striking recent advances in protozoan morphology and leaves the problem of the origin of the metazoan centrosome very much as it was ten years ago.

The pioneer work of Schaudinn's upon which this conception of Hartmann and Prowazek's is based has not been fully and satisfactorily confirmed, while much of it has been denied. Novy, for example, has continually fought against the double intra- and extra-cellular life of *Trypanosoma noctuæ* and now Moore and Breinl,[2] working with different kinds of *Trypanosoma*, find that the nuclei of *T. gambiense*, *T. brucei* and *T. equinum* all conform to the centronucleus type and that the blepharoplast or kinetonucleus (Woodcock) arises in the latent bodies by halving of the intra-nuclear division center and without any accompanying chromatin such as Schaudinn described in the case of *T. noctuæ*. Passing over the fact that the present authors somewhat stultify themselves on the perfection of their technique and give an ungenerous blanket criticism of all others who have worked upon the morphology of trypanosomes, it must be admitted that their criticism is to a certain extent justified, for the majority of observers have made too free use of the dry smear method. The so-called chromosomes of the trypanosomes, for example (not chromosomes at all in the strict sense), are interpreted by Moore and Breinl as irregular masses of chromatin which may assume any form under the rough processes of the dry method of fixation. This may or may not be true, but at any rate the figures given by the English authors and representing the finer structures of these nuclei do not inspire confidence in the methods which they themselves advocate, although they are, indeed, well tried and recognized methods.

[2] Moore and Breinl. Cytology of the Trypanosomes. *Annals of the Liverpool School of Tropical Medicine*, 1, No. 3.

Apart from this question of technique, upon which the last word is not yet given, Moore and Breinl bring forward evidence which throws a new light on the life history of *T. gambiense*, the cause of sleeping sickness. They find a phase in the life history where the nucleus, surrounded by a small bit of protoplasm, is left over after the bulk of the trypanosome has degenerated. This nucleated bit, which they name the "latent body," is stored up in the spleen and bone marrow of the experimental animal (rat), ultimately reappearing in the circulation where a new, young trypanosome arises from it. They find no evidence of trimorphic differentiation which Schaudinn first described for *T. noctuæ*, but they call attention to the fact that a complete series of sizes of trypanosoma may be selected, and claim that the indifferent, male, and female, forms are only arbitrarily chosen individuals from such a series.

Another interpretation is given to the trypanosomes with long chromatin bars such as Prowazek in the case of *T. lewisi* regarded as male forms. The English observers introduce a new hypothesis to account for this, viz., that it represents a type of autogamous conjugation. The bar is of kinoplasmic material growing out from the blepharoplast to the nucleus, where a portion of its substance, as they believe, unites with the nucleus. The suggestion is ingenious and, in view of the constantly growing evidence in favor of autogamy in other kinds of protozoa (Entamœba, Actinosphærium, *Amœba proteus*, etc.), must be taken into account.

On *a priori* grounds it would certainly seem that if conjugation among trypanosomes is a normal part of the life history, and there is no reason to believe it absent, it would be more frequently observed and there would be no uncertainty about it. Its infrequency and the doubt existing in regard to the observations that have already been made lead us to suspect that conjugation of some obscure type occurs here. In flagellated protozoa where conjugation of the ordinary type is characteristic, the periodicity of conjugation is one of the most noteworthy features. This is well illustrated in a timely article by C. Clifford Dobell on the life history of a simple Peranema-like flagellate which he names *Copromonas subtilis*.[3] The flagellate is a com-

[3] Dobell, C. Clifford. The Structure and Life History of *Copromonas subtilis* nov. gen. et nov. sp., a Contribution to our Knowledge of the Flagellata. *Q. J. M. S.*, No. 205, 1908.

mon parasite of the rectum of frogs and toads and grows readily, the author observes, in rectal contents with normal salt. Conjugation between similar organisms (isogametes) occurs from the seventh to the ninth day of such a culture, the result being either an encysted form (permanent cyst) or a motile form which reproduces by division for several generations and then encysts.

The trypanosomes evidently present no such simple life history as this which Dobell describes and, although accumulating evidence makes it probable that all stages are confined to the single host in the greater number of cases at least, every description of conjugation thus far published is so fantastic as to arouse suspicion. What is true of trypanosomes is even more characteristic of spirochætes, a field of research so difficult that very few have had the hardihood to publish accounts of conjugation, and needless to say none that has been published is acceptable. The latest on Spirochæta is a paper by H. B. Fantham on the relatively large spirochæte of the oyster and clam.[4] This *Spirochæta balbianii*, which was monographed by Perrin a couple of years ago, is interesting in having a central helix of chromatin which is spirally wound, and upon which larger granules of chromatin are suspended at intervals. This represents an intermediate condition, so far as the nucleus is concerned, between the isolated granules of chromatin in bacteria and in certain forms of Spirochæta (*e. g.*, *S. obermeieri*), and the formed nuclei of higher types of protozoa. Reproduction both of this form and of *S. anodontæ* is by longitudinal and occasionally transverse division, both types occurring according to the author. Conjugation in no form was observed. Like the majority of recent writers on the spirochætes, Fantham proposes a new group for them intermediate between the protozoa and the bacteria. He suggests that they be made a new "class" of organisms under the name "Spirochætacea." Such innovations, however, can do no good and it is far better not to further confuse an already mixed up classification. When the full life history of the genus (or genera) of Spirochæta is known it will be time enough to change the classification.

These flagellates are not the only forms of protozoa over

[4] Fantham, H. B. *Spirochæta* (*Trypanosoma*) *balbianii* (Certes) and *Spirochæta anodontæ* (Keysselitz). Their Movements, Structure and Affinities. *Q. J. M. S.*, No. 205, 1908.

which there is much discussion and controversy at the present time. The rhizopods offer quite as extensive a field for divergent opinions and here again it is mainly in connection with the parasitic types. The life histories of the ordinary forms are being slowly established and with this basis the parasitic forms should be comparatively simple to work out. The one remaining important step to be made in working out the life history of the common rhizopod *Arcella vulgaris* has quite recently been taken by W. Elpetiewsky,[5] and it is fitting that it should have been made in Hertwig's laboratory, where the first important steps were taken. The author finds that gametic nuclei are formed from the distributed chromidia in the way described by Schaudinn for Centropyxis, and by Schaudinn and Lister for Polystomella. Macrogametes and microgametes are formed and conjugation of two such anisogamous swarmers was followed step by step. He found furthermore, that Arcella reproduces also by the formation of pseudopodiospores, and that these develop fine heliozoa-like radiating pseudopodia, upon the ends of which they roll about for a period of from two to three hours. This observation is interesting in the light of the possible origin of the lobose rhizopods from the heliozoa.

It is not quite so simple a matter to accept the latest work on the parasitic rhizopods and we entirely disagree with Prowazek[6] in his conception of the so-called group Chlamydozoa. In this proposed new group of protozoa which he would place intermediate between the protozoa and the bacteria, Prowazek places the majority of the recently contested forms of disease-producing organisms. The disputed organisms of variola, vaccinia, scarlet fever, trachoma, rabies, *Molluscum contagiosum*, and some others of less importance are all grouped together here apparently without regard to their morphology or effects upon the host. All of these organisms are regarded as extremely small cell parasites which are made conspicuous by reason of a more or less thick secretion of nuclear material about them, the name of the proposed group being based upon this characteristic (χλαμυς—mantle).

In this supposition the author takes a great deal for granted and begs two very important questions, first, that the inclusions

[5] W. Elpetiewsky. Zur Fortpflanzung von *Arcella vulgaris* Ehr. in *Arch. f. Prot.*, X, No. 2–3, 1907.

[6] S. Prowazek. Chlamydozoa. In *Arch. f. Prot.*, X, No. 2–3, 1907.

are organisms, and second, if organisms, that the bulk of their substance is to be traced to nuclear secretions. The limits of the present reference will not permit an extensive analysis of Prowazek's different assumptions, but one or two matters may be pointed out as showing his method of treatment, and incidentally his ignorance or, possibly, disregard, of careful work of others. The organism of rabies, for example, exists, as do all rhizopod protozoa in many different sizes, and one form of the organism is extremely minute. This small phase is characteristic of the so-called "fixed virus" and has been entirely overlooked by Prowazek despite the accurate and detailed work of Dr. A. W. Williams and others. In another phase the organism is quite large and characteristically amœboid in form. Prowazek finds none of these larger forms in centrifuged virus and concludes that the intra-cellular phase is absent in the virus thus treated, and since he failed to see these forms in the fixed virus he further concludes that the bulk of the Negri body in rabies must be a nuclear secretion and that the organisms are the minute brightly staining points (chromatin) of the larger forms which are actually present in the fixed virus and in centrifuged virus, but invisible. In this conclusion he shows not only a total disregard for what other competent workers have done, but a surprising ignorance of the actual structure of the Negri body.

Apart from special criticisms which might be carried out for each of the diseases mentioned, the general criticism may be made that it is not good zoology to create a group in classification while there is still some doubt as to the organisms being living things; and it is not good cytology to assume an entirely new function (of specific secretions) in various cells in response to such questionable organisms. The present critic believes, indeed, that these questionable structures are organisms, and organisms belonging to the rhizopod group of protozoa, but not to any group with the characteristics of the proposed "Chlamydozoa."

G. N. C.

EXPERIMENTAL ZOOLOGY

The Determination of Sex in Frogs.—Few results in experimental biology have been more puzzling than those involving the question of the determination of the sex of the frog. The earliest

observations—those of Born—seemed to indicate that the food given to the young tadpoles determined the sex of the frog. Yung also obtained about 70 per cent. of females when his tadpoles were well fed. Balbiani and Henneguy have stated that tadpoles fed on egg-yolk produced more females than those fed on a vegetarian diet. On the other hand, Cuénot obtained no such results, and the recent careful and extensive experiments of Miss King have shown clearly for the toad that the nutrition of the tadpole has no influence on the sex of the adult. Despite the fact that these recent results go far towards showing that sex is not determined or even altered by food relations, a curious disproportion of the sexes in frogs has been noted by several observers. The recent valuable experiments of Richard Hertwig do not, in the opinion of the reviewer, bear out the interpretation that Hertwig has placed upon them. Nevertheless, his methods give promise, if further extended, of throwing light on the problem.

In Hertwig's first contribution to the subject published in 1906 he suggested that sex is determined by the condition of *ripeness* of the egg at the moment of fertilization. This view is not new, and Hertwig's attempt to connect his view with the ratio of nucleus to cell-plasm of the egg at different periods of its maturation can hardly be looked upon favorably, since in the frog's egg the nucleus as such has already disappeared when the egg leaves the ovary. The chromosomes are thereafter arranged on the equatorial plate of the first polar spindle. It is, however, during this period that the degree of ripening is supposed to determine the sex of the egg. However unsatisfactory this specific suggestion of Hertwig may now appear, the possibility must still be granted that in some way the degree of maturity of the egg may have an influence on sex-determination. Hertwig interpreted his experiments to mean that at first the egg *tends* to produce males, then during the middle phases of its ripening it tends to produce females, and finally during its later phases again its tendency is towards male production. It is not our purpose to discuss in detail this interpretation, but it may be stated that Hertwig's experiments fell far short of proving his hypothesis.

In Hertwig's second paper,[1] to which we wish more especially

[1] Hertwig, R. Weitere Untersuchungen ueber das Sexualitätsproblem. *Verh. Deutsch. Zool. Gesell.*, 1907.

to call attention, he also brings forward the same hypothesis and attempts to explain certain incongruities of the two series by other suggestions. It will be noticed that while the "older" eggs give an enormously high percentage of males, those first fertilized also give an excess of males or at least equal numbers of the two sexes. There is no middle register in which females are in excess.

Hertwig's principal results are shown in the accompanying table. The eggs of three females, 1, 6, and 10, were fertilized at four different intervals (I, II, III, IV) of several hours apart (6, 18, 30, etc.); the percentages show in each case how many males developed to each 100 females—the actual number of individuals employed standing above the percentages. The striking fact shown by the table is the high percentage of males throughout, but especially towards the end of each series, where in one case there were 129 males to 17 females.

	I		II		III		IV
		—6—		—18—		—30—	
1.	34♀ : 47♂		65♀ : 77♂		156♀ : 194♂		7♀ : 48♂
	141%		119%		124%		685%
		—36—		—18—			
6.	64♀ : 61♂		101♀ : 139♂		115♀ : 169♂		
	95%		137%		147%		
		—18—		—24—		—22—	
10.	55♀ : 52♂		148♀ : 87♂		71♀ : 70♂		17♀ : 129♂
	100%		59%		100%		759%

The results leave little doubt that there is something in this series that stands for maleness. A number of possibilities besides the one adopted by Hertwig will suggest themselves. There is, moreover, one vital weakness in the experiment as carried out, for which, unfortunately, there is no control—different males were used, apparently, at least for the last fertilization, and the percentage of male-producing sperm present in these males was not determined. Without this control the experiment is seriously defective. Hertwig himself has realized this deficiency and has carried out one successful experiment in which the eggs of one female—separated into lots—were fertilized by different males. The results are not convincing, as the following statement shows.

The eggs of a female from a locality (Lochausen, indicated by L in the table), where the season was nearly at its end, were separated into six lots. Three of these were fertilized by sperm

from three males of the same locality (indicated by l^1, l^2, l^3, in the table), and the other three were fertilized by sperm of three males from another locality (Schleissheim, — S in diagram). The converse experiment was also carried out. The results are given in the next table, in which the double sign ♀♂ indicates that the sexual organs were in an indifferent condition. It will be observed that a very large number of individuals are referred to this category. Hertwig states that in those cultures that developed best there was a decided excess of males—more than of indifferent forms. On the other hand, the poor cultures contained females almost exclusively, fewer indifferent forms and no males.

	l'	s'	l^2
L.	2♀♂ : 31♀	9♀♂ : 53♀	80♂ : 77♀♂
S.	9♀♂ : 65♀	†	77♂ : 73♀♂
	s^2	l^3	
L.	176♂ : 156♀♂	———————	
S.	10♂ : 75♀♂	9♂, 59♂♀ : 65♀♂, 11♀	

Hertwig thinks that the results show that the sperm has a distinct influence on sex-determination. He suggests that in the present case the eggs were nearly in a condition of equilibrium so that a *slight* influence on the part of the male sufficed to turn the scales. He adds that it is thinkable that as a rule the eggs at the time of normal fertilization have their sex so positively determined that the relatively small influence of the male has no influence. It will be noted, however, that in Hertwig's own experiment the condition of the two females selected was very different, yet there is a surprising similarity in the results produced when the males that fertilized the eggs are considered.

The experimental results are not sufficient to give any positive light on the question, but the method that Hertwig has employed in the last experiment is one that promises to give an answer to the question whether the egg or the sperm determines the sex in the frog.

If one may hazard a guess, the results of Hertwig's experiments seem to show that the male is responsible for sex-determination. Since normally all the eggs are fertilized it can not be assumed that, if they are of two sexes, those of one sex are preponderatingly injured or killed by the cold of winter. In regard to the sperm, however, it is possible that more of one kind,

if two kinds exist, are injured or that internal processes may lead to the production of more functional sperm of one sex. These factors may differ in different individuals or be characteristic of different races or regions. The importance of settling this question and the ease with which the experiment can be carried out with the simplest possible apparatus ought to lead many naturalists to repeat the experiment in different localities and with different species. The only difficulty arises from the mortality of the tadpoles; for they must be kept until the time of metamorphosis (which, however, for the wood frog, the toad and for some of the tree frogs takes place as early as June of the same year). By keeping the tadpoles in running water, or by changing the water in the dishes every day, success is assured.

M.

ANATOMY

Wiedersheim's Comparative Anatomy.[1] The various forms and editions of this work have been for two decades, we believe, the most used and useful text-books upon the comparative anatomy of vertebrates. In the ten years since the publication of the second English edition, three progressively larger German editions have appeared, and the book became so large that Wiedersheim published a résumé entitled "An Introduction to Comparative Anatomy." The third English edition is, in both size and substance, a compromise between the second English and the large German editions. The text proper occupies one hundred and ten pages more than in the second edition. This is due partly to the addition of new matter and partly to the use of uniform type in the text, instead of printing in smaller type the matter assumed to be less worthy of the student's attention. This change has improved the appearance of the book and the increase in size has been partly counterbalanced by printing more compactly and in smaller type the much extended and useful bibliography.

New facts have been incorporated, usually and unfortunately without recasting, but the sections upon the skin, skull, brain-

[1] Comparative Anatomy of Vertebrates. Adapted from the German of Dr. R. Wiedersheim, by W. N. Parker. Third edition, founded on the sixth German edition. 576 pp., 372 figures. The Macmillan Company, 1907.

membranes and "adrenals" have been essentially rewritten. As a result, the book is improved by many small increments as well as by the new treatment of a few subjects.

Among these is the interesting physiological difference between the lungs of birds and of mammals, now properly noted for the first time. In mammals during inspiration the lung expands and draws into its blind terminal respiratory chambers a mixture of fresh and residual air. The residual air greatly dilutes the oxygen which comes in contact with the absorbing blood vessels, and also prevents the carbon dioxide from being expired directly. In birds the lung is a network of anastomosing tubes which are not expansile. Fresh air is drawn through these tubes by the expansion of the air sacs, which are non-respiratory terminal prolongations of the lung. The lung of the bird may, in a sense, be compared with the respiratory bronchioles of mammals, the mammalian alveoli corresponding with the avian air sacs. Thus the lung of birds is peculiarly adapted for the rapid oxidation correlated with the requirements of flight and with a high body temperature. Other additions of this sort contribute to the value of this edition.

L. W. Williams.

(No. 492 was issued January 23, 1908.)

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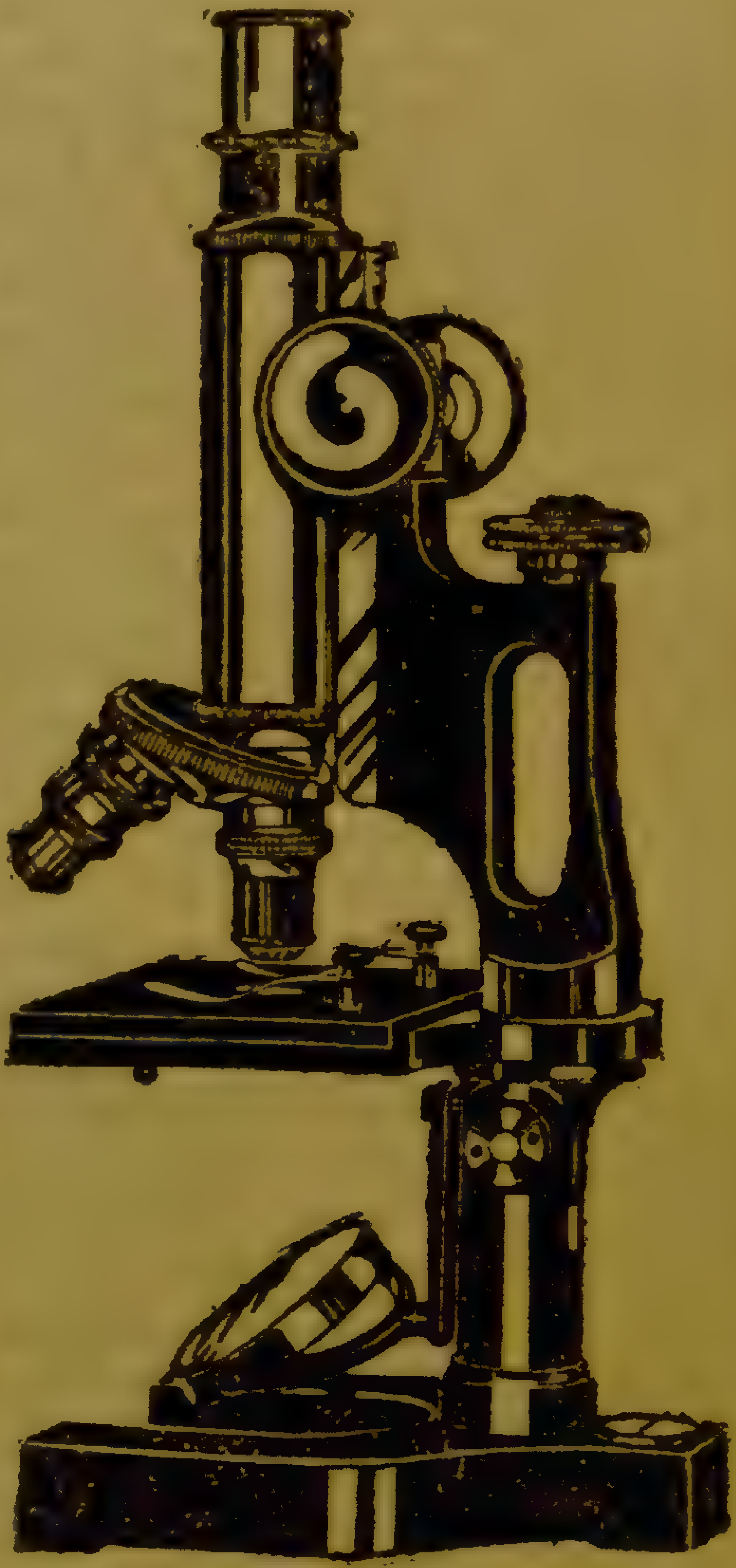

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Boston Society of Natural History,
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GLOVER M. ALLEN, *Secretary*

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THE
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THE LAW OF GEMINATE SPECIES

PRESIDENT DAVID STARR JORDAN
Stanford University

In "Evolution and Animal Life," by Jordan and Kellogg (page 120), the following words are used:

> "Given any species, in any region, the nearest related species is not to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort or at least by a belt of country, the breadth of which gives the effect of a barrier."

Substituting the word "kind" for species in the above sentence, thus including geographical subspecies, or nascent species, as well as species clearly definable as such, Dr. J. A. Allen accepts this proposition as representing a general fact in the relations of the higher animals. To this generalization Dr. Allen, in a late number of *Science*, gives the name of "Jordan's Law." The present writer makes no claim to the discovery of this law. The language above quoted is his, but the idea is familiar to all students of geographical distribution and goes back to the master in that field, Moritz Wagner.

This law rests on the fact that the minor differences which separate species and subspecies among animals are due to some form of segregation or isolation. By some barrier or other the members of one group are prevented from interbreeding with those of another minor group or with the mass of the species. As a result, local peculiarities arise. "Migration holds species true, localiza-

tion lets them slip,'' or rather leaves them behind in the process of modification. The peculiarities of the parents in an isolated group become intensified by in and in breeding. They become modified in a continuous direction by the selection induced by the local environment. They are possibly changed in one way or another by germinal reactions from impact of environment. At last a new form is recognizable. And this new form is never coincident in its range with the parent species, or with any other closely cognate form, neither is it likely to be in some remote part of the earth. Whenever the range of two such forms overlaps in any degree, the fact seems to find an explanation in reinvasion on the part of one or both of the forms. The obvious immediate element in the formation of species is, therefore, isolation, and behind these are the factors of heredity, of variation, of selection, and others as yet more or less hypothetical involved in the effect of impact of environment on the germ cells themselves. The formation of breeds of sheep as noted by Jordan and Kellogg (p. 82), seems exactly parallel with the formation of species in nature. In like manner, the occasional development of breeds arising from the peculiarities of individuals is possibly parallel with the ''mutations'' of the evening primrose. Such breeds are the Ancon sheep in Connecticut and the blue-cap Wensleydale[1] sheep in Australia. The ontogenetic species—groups in which many individuals are simultaneously modified in the same way by like conditions of food or climate—show no permanence in heredity. Such forms, however strongly marked, should, therefore, have no permanent place in taxonomy. The recent studies of Mr. Beebe on the effects of moist air in giving dusky colors to birds serve to illustrate the impermanence of the groups or subspecies characterized by dark shades of color developed in regions of heavy rainfall.

It may also be noted in passing that one cause of the

[1] Blue Cap, a ram of Leicester-Teeswater parentage, having a blue shade on his head, was the progenitor of a breed having this peculiarity, known as the Wensleydale, in Australia.

potency of artificial selection among domesticated animals or cultivated plants is that such selection is always accompanied by segregation. The latter is taken for granted in discussions of this topic and hence its existence as a factor is usually overlooked. While poultry or pigeons can be rapidly and radically changed by artificial selection, in isolation, no process of selection without isolation is likely to have any permanent result. For example, we know no way of improving the breed of salmon, because the salmon we have selected for reproduction must be turned loose in the sea, where they are at once lost in the mass.

New forms of gold-fish and carp can be made easily in domestication, because these fishes can be kept in aquaria or in little ponds, but new forms of mackerel or herring are beyond the control of man and the species actually existing have been of the slowest creation, their origin lost in geologic times.

One of the most interesting features of "Jordan's law" is the existence of what I may term *geminate* species—twin species—each one representing the other on opposite sides of some form of barrier. In a general way, these geminate species agree with each other in all the respects which usually distinguish species within the same genus. They differ in minor regards, characters which we may safely suppose to be of later origin than the ordinary specific characters in their group. Illustrations of geminate species of birds, of mammals, of fishes, of reptiles, of snails, or of insects, are well known to all students of these groups, and illustrations may be found at every hand.

Each island of the West Indies, which is well separated from its neighbors, has its own form of golden warbler. Each island in the East Indies has its geminate forms of reptiles or fishes. Each island of the Hawaiian group has its own representative of each one of the types or genera of Drepanidæ. Each group of rookeries in Bering Sea has its own species of fur seal.

One of the most remarkable cases of geminate species

is that of the fishes on the two sides of the isthmus of Panama. Living under essentially the same conditions, but separated since the end of the Miocene Period by the rise of the isthmus, we find species after species which has been thus split into two. These geminate species, a hundred or more pairs in number, were at first regarded as identical on the two shores of the isthmus. Later one pair after another was split into recognizable species. The latest authority on the subject, Mr. C. T. Regan, seems to doubt if any species of shore fishes are actually identical on the two sides of the isthmus.

To make this clear, though at the risk of being tedious, I give below a partial list of these geminate species about the isthmus of Panama:

Atlantic Coast	Pacific Coast
Harengula humeralis	*Harengula thrissina*
Clupanodon oglinus	*Clupanodon libertatis*
Centropomus undecimalis	*Centropomus viridis*
Centropomus pedimacula	*Centropomus medius*
Centropomus affinis	*Centropomus ensiferus*
Epinephelus adscensionis	*Epinephelus analogus*
Alphestes afer	*Alphestes multiguttatus*
Dermatolepis inermis	*Dermatolepis punctatus*
Hypoplectrus unicolor	*Hypoplectrus lamprurus*
Lutianus cyanopterus	*Lutianus novemfasciatus*
Lutianus apodus	*Lutianus argentiventris*
Lutianus analis	*Lutianus colorado*
Lutianus synagris	*Lutianus guttatus*
Hæmulon album	*Hæmulon sexfasciatum*
Hæmulon parra	*Hæmulon scudderi*
Hæmulon schrancki	*Hæmulon steindachneri*
Anisotremus suriamensis	*Anisotremus interruptus*
Anisotremus virginicus	*Anisotremus tæniatus*
Conodon nobilis	*Conodon serrifer*
Pomadasis crocro	*Pomadasis branicki*
Calamus macrops	*Calamus taurinus*
Xystæma cinereum	*Xystæma simillimum*
Encinostomus pseudogula	*Encinostomus dowi*
Kyphosus incisor	*Kyphosus analogus*
Isopisthus parvipinnis	*Isopisthus remifer*
Nebris microps	*Nebris zestus*
Larimus fasciatus	*Larimus pacificus*

Atlantic Coast	Pacific Coast
Odontoscion dentex	*Odontoscion xanthops*
Corvula sialis	*Corvula macrops*
Bairdiella veræ-crucis	*Bairdiella armata*
Micropogon furnieri	*Micropogon ectenes*
Umbrina broussoneti	*Umbrina xanti*
Menticirrhus littoralis	*Menticirrhus elongatus*
Eques acuminatus	*Eques viola*

This list may be greatly extended, but the series noted will illustrate the point in question. Whenever a distinct and sharply defined barrier exists, geminate or twin species may be found on the two sides of it, unless, as sometimes happens, the species has failed to maintain itself on one side of the barrier. So far as Panama is concerned, we have evidence that the barrier was raised near the end of Miocene time with no trace of subsequent depression. We can thus form some estimate of the age of separation in at least a small number of closely related species. In this and similar cases it is not possible to conceive of the formation of these species by sudden mutation, or that they would retain their separate existence were the element of segregation removed. While segregation or isolation is not a force, and perhaps not strictly a cause in species formation, it is a factor which apparently can never be absent, if the species retains its independent existence.

There is no doubt that the distribution of higher animals in general is in accord with "Jordan's Law." Examples by the thousand come up from every hand. If we had a hundredth part of the amount of available evidence in support of mutation theories, these theories would pass from the realm of hypothesis into that of fact. But the application of this law or rule to plants and to one-celled animals has been questioned. So far as rhizopods are concerned, Dr. Kofoid finds that the species are in general sharply defined and of the widest distribution in the sea, so that we can hardly state laws as defining their geographical distribution. To these minute floating animals, the sea scarcely offers barriers at all, and the recognized species do not seem to be products of geographical iso-

lation. Doubtless these species in duration and in nature correspond more nearly to genera or families of higher animals than to actual species. Perhaps minor specific differences such as we note among arthropods or vertebrates are intangible or non-existent. The effects of isolation may be tangible only among forms which possess more varied relations with their environment.

The application of this law to plants has also been denied. But geminate species are just as common in botany as in zoology, and the effects of isolation in species-forming are just as distinct. The law is just as patent in the one case as in the other. It is merely obscured by other laws or conditions which obtain among plants.

In the nature of things, most physical barriers are more easily crossed by plants than by animals. The possibilities of reinvasion are thus doubtless much increased. The plant is limited by climate, rainfall, nature of soil, and the same species is likely to occupy all suitable locations within a large area. Animals are more mobile than plants within their range, a fact which tends to keep the interbreeding masses more uniform. In the struggle for existence, the plant is pitted against its environment. Whether a plant survives or not depends not much on the nature of the seed, but mainly on its relation to the spot on which it falls. There is little selection within the species due to the choice of one individual as against another. This can only happen where plants are overcrowded, and there the survival is mainly that of the seed whose roots run deepest. There is little room for struggle between closely related species. Each individual grows—if it can—on the spot where it falls. The variations among plants are great, but these variations are mostly lost unless reinforced by segregation. There is no likelihood of the survival of DeVries' mutants of the evening primrose if these forms are left free to mix in the same field.

Among plants we often notice the fact—rare though not unknown among animals—of numerous species of the same genus occupying the same area. In some cases these

species are closely related, suggesting mutants, and in other cases the relation indicates the existence of hybrids. In California, for example, there are in the same general region many species of Lupinus, of Calochortus, of Ceanothus, of Arctostaphylos, of Eschscholtzia, of Godetia, of Œnothera, and Opuntia. Eucalyptus, Acacia and Epacris in Australia are examples even more striking. But I have never seen very closely related or geminate forms in any of these genera actually growing together. I suspect that they do so sometimes and that the explanation is found in reinvasion. But "growing together" is an indefinite statement as applied to plants. The elder, the alder and the madroño (arbutus) abound in the Santa Clara Valley. But no one ever saw any two of these trees standing side by side. Each has its limitations, as to soil and moisture.

Setting aside these genera which are represented by many species in a limited area, and among which mutation and hybridism may be conceivably factors in species-forming, we find the law of geminate species applying to plants as well as to animals. Crossing the temperate zone anywhere on east and west lines, we find species after species replaced across the barriers by closely related forms. Illustrations may be taken anywhere among the higher plants—equally well, no doubt, among lower ones. Many genera are local in their distribution, monotypic—with a single species, the origin of which can not be traced. But many other genera belt the earth or come very near doing so, each form or species being geminate as related to its next neighbor. This fact is illustrated in Rubus, Alnus, Sambucus, Platanus, Fagus, Veratrum, Symplocarpus, Symphoricarpus, Castanea, Quercus, Pinus, Tsuga, Acer, Rhus, Pyrus, Prunus, Lonicera, Ranunculus, Trientalis, Lilium, Trillium, Veronica, Aquilegia, Gentiana, Viola, Epilobium, Pteris, Mimulus, Trifolium, Solidago, Aster. All these genera and many others furnish an abundance of examples.

We may, therefore, say that with plants as well as animals geminate species as above defined owe their dis-

tinctness to some form of isolation or segregation, and that, broadly speaking, with occasional exceptions, given any form of animal or plant in any region, the nearest related form is not to be found in the same region nor in a remote region, but in a neighboring region, separated from the first by a barrier of some sort, not freely traversable.

A law, that is, an observed relation of cause and effect is not invalidated by the presence of other effects due to other causes, in the same environment. The actual conditions in nature are everywhere not products of single and simple forces, but resultants of many causative influences, often operative through the long course of the ages.

It may be urged that these geminate groups or forms are not true species, because they often intergrade one into another, and they would probably be lost by intermingling if the barriers were removed. It is sometimes claimed that only physiological tests of species can be trusted, as true species will not blend and their hybrids, if formed, will be sterile. All this is purely hypothetical and impracticable to the systematic zoologist, and not of much value to the botanist. Closely related species can usually be readily crossed. As the relation becomes less close, partial sterility of all grades and then total sterility appear.

Species as we find them in nature are real *species* if that term has any definition. And real species have, as a rule, indefinite boundaries, shading off into subspecies, geminate species, ontogenetic forms and the like. And if we are to understand the significance of nature, we have to describe these facts and relations as they actually are. Then we have to find out what changes we can work in individuals and in species by such alterations of conditions as experiment can give.

We do not know actually any species of animal or plant until we know all changes that would take place in its individuals under all conditions of environment.

FASCIATIONS OF KNOWN CAUSATION

DR. HENRI HUS

Missouri Botanical Garden

Among plants, whether in the garden or in the field, individuals occur with greater or less frequency, which, because they exhibit a striking departure from the accustomed form, attract immediate attention. To denote such abnormal forms, the term "teratological" is used. Teratology covers a wide field. It includes the deviations from the usual arrangement of the parts, such as the union of organs and alterations of position, as well as deviations from the form, number and size of the parts of the plant. Frequently an explanation does not readily offer itself, at other times the inciting cause is demonstrated without trouble.

Though it is only in comparatively recent years that the true value of the study of abnormal forms has been realized, it must not be thought that in the earlier days the subject was overlooked. Numerous papers on teratological cases were published during the seventeenth century, for instance that by Wurffbain.[1] The eighteenth century saw an increase in the number of similar publications. Even Linnæus, before he enunciated his "varietates levissimas non curat botanicus," seems to have devoted some time to the study of abnormal forms.[2] At the same time, it was not until 1814 that the first collective publication on this subject, covering more than 300 pages and containing several illustrations, appeared.[3] This, at greater or lesser intervals, was followed by others, the

[1] Wurffbain, Johannes Paulus. De folia lactucæ monstroso. "Miscell. Acad. Nat. Curios.," Dec. 2, A. 10, 411, 1691.

[2] Linnæus, Carolus. Pommerantz med et inneslutit foster. "Vetensk. Akad. Handl.," A. 281, 1745.

[3] Jaeger, G. F. Ueber die Missbildungen der Gewächse. Stuttgart, 1814.

most important being those of Schlotterbeck,[4] Engelmann[5] and Moquin-Tandon.[6] Since the middle of the last century numerous smaller papers on teratological subjects have appeared. The earlier data have been collected by Masters[7] and by Penzig,[8] in the former publication the abnormalities being arranged according to kind, in the latter under the various families, genera and species.

The main point of interest in abnormal forms lies not in the mere fact of the existence of the abnormalities nor in the extremes which they may reach, but rather in the light thrown by them upon plant development,[9] and they are therefore entitled to equal consideration with hybridization[10] which, as de Vries[11] has pointed out, permits the analysis of the specific characters and thereby makes possible the study of a single character, since the plant is to be considered merely as an expression of the reaction of elementary units, sometimes occurring singly, at other times in groups.

Among the plant monstrosities which are most frequently observed are fasciations, in which more often the stems, but sometimes other parts of the plant, appear to broaden and assume a flat appearance. Their existence has been known for centuries, for instance the fasciation of *Sedum reflexum* (*S. crispum*), illustrated by Munting[12]

[4] Schlotterbeck, P. J. Schediasma botanicum de monstris plantarum quo analogiam regno vegetabili cum animali intercedentem in producendis iisdem adstruit et figuris illustrat. *Acta Helvetica,* 2: 1, 1816.

[5] Engelmann, G. De Antholysi Prodromus. Frankfurt a. M., 1832.

[6] Moquin-Tandon, A. Éléments de Tératologie Végétale. Paris, 1841.

[7] Masters, M. T. Vegetable Teratology, London, 1869.

[8] Penzig, O. Pflanzen Teratologie. Genua, 1890–1894.

[9] Goebel, K. Bedeutung der Missbildungen für die Theorie der Organbildung. Organographie der Pflanzen, 173, 1898–1901.

[10] Tschermak, E. The Importance of Hybridization in the Study of Descent. Report of the Third International Conference on Genetics. Royal Horticultural Society, 278–284, 1906.

[11] de Vries, Hugo. Intracellulare Pangenesis. Jena, 1889. Sur les unités des charactères spécifiques et leur application a l'étude des hybrides. *Rev. gén. bot.,* 12: 257, 1900.

[12] Munting, A. Waare Oeffeninge der Planten, 1672.

and in numerous species, in fact, in so many species, in so many genera and in so many families, among fungi, among gymnosperms, among monocotyledons and dicotyledons, on herbs, on shrubs and on trees, that the assumption appears justified that fasciation may be expected to make its appearance at some time, in some part, in any species. This is the view held by Sorauer,[13] but de Vries[14] does not make so sweeping a statement.

Fasciations may be propagated vegetatively, for instance, by means of tubers, as in *Oxalis crenata*[15] or through cuttings, as was done at the Missouri Botanical Garden for fasciations of the tomato, *Solanum Lycopersicum*, snap-dragon, *Antirrhinum majus*, hen-and-chickens, *Echeveria glauca* and others. Fasciations may also be transmitted through seed. Among the best known instances is the cockscomb, *Celosia cristata* and its varieties, which, because of this abnormality, is cultivated in gardens. It is a form which, like the cockscomb amaranth, *Amaranthus cristatus*, has been known for centuries to exist, and is always propagated through seed. Recently it has again been shown for Munting's *Sedum reflexum*[16] as previously by de Vries.[17]

The possibility of the transmission of the fasciated character to the offspring, had already been recognized by Godron[18] who, however, says: "Les fasciés sont rarement héréditaires et jamais d'une manière absolue." While the truth of the latter part of the statement has been borne out by subsequent work, in the light of experiments carried on during the last twenty years, and especially those of de Vries,[19] the first part should be amended.

[13] Sorauer, P. Handbuch der Pflanzen-krankheiten, 1[3]: 334, 1906. "Die Fähigkeit zur Fasciation ist bei allen Pflanzen voraus zu setzen."

[14] De Vries, Hugo. Die Mutationstheorie, 2: 551. Leipzig, 1901–1903.

[15] 17th Ann. Rep. Missouri Botanical Garden, 147, 1906.

[16] Von Wettstein, R. Die Erblichkeit der Merkmale von Knospenmutationen. Festschrift zu P. Ascherson's Siebzigstem Geburtstage, 509, 1904.

[17] Mutationstheorie, 1: 128.

[18] Godron, A. Mélanges de Tératologie Végétale. *Mém. Soc. d. Sc. Nat. d. Cherbourg*, 16: 97, 1871–1872.

[19] De Vries, Hugo. Over de erfelykheid der fasciatien. Avec un résumé en langue française. *Bot. Jaarb. Dodonæa*, 6: 72, 1894.

We have a right to believe that fasciations, like other monstrosities, with the exception, perhaps, of some cases of virescence,[20] may be inherited, though not by all descendants. Else such varieties could not be offered on the exchange list of the Amsterdam botanic garden as *Aster Tripolium fasciatum, Geranium molle fasciatum, Picris hieracoides fasciata, Veronica longifolia fasciata* along with *Chrysanthemum segetum fistulosum,* in which the ligulate florets have become tubular like the disk flowers, *Dipsacus sylvestris torsus,* which has a twisted stem, *Lychnis vespertina glabra,* which lacks the trichomes on the pod, etc.[21] But it must be remembered that good soil, great care, especially in the earlier stages, plenty of room—in one word, optimum conditions only—give the desired result.

Of far greater interest, at the present time at least, is the consideration of the causes of fasciation and its exact nature. Two kinds of fasciation appear to be possible. The one is caused by the combination, in a plane, of several axes, according to Lopriore.[22] The other mode of fasciation, far more common, and the one which will be considered here, consists of the flattening of the stem through a broadening of its apical cone into a comb, as shown by Nestler,[23] who did his work at the laboratory

[20] De Vries, Hugo. Een epidemie van vergroeningen. Avec un résumé en langue française. *Bot. Jaarb. Dodonæa,* 8: 66. 1896.

In at least one case, that of the green-flowered *Oxalis stricta,* it has been shown that virescence may be transmitted through the seed (18th Ann. Rep. Missouri Botanical Garden, 99, 1907). The third observed, generation of these plants, now (January, 1908) in flower in the greenhouse, still shows the typical character. Now, as formerly, there is no sign of insects to which the cause of the virescence could be attributed.

[21] De Vries, Hugo. Erfelyke monstrositeiten in den ruilhandel der botanische tuinen. Avec un résumé en langue française. *Bot. Jaarb. Dodonæa,* 9: 62, 1897.

[22] Lopriore, G. I caratteri anatomici delli radici nastriforme. Ex. in *Zeitschr. f. Pflanzenkr.,* 14: 226, 1904.

''Solche bandförmige Nebenwurzeln entstehen entweder durch dichtes Aneinanderschlieszen mehrerer senkrecht übereinanderstehenden zylindrischen, oder durch gleichsinnige Verwachsung der Zentralzylinder mehrerer Seitenwurzeln, die sich mit einer gemeinsamen Rinde umgeben.''

[23] Nestler, A. Untersuchungen über Fasciationen. *Oester. Bot. Zeitschr.,* 44: 343, 1894.

for plant physiology at Amsterdam under the direction of de Vries. That we are dealing with but a single branch, and not several, though frequently the ribbed appearance of a fasciation gives cause to think otherwise, is well shown by Sorauer[24] in the case of a fasciation of the Norway spruce, *Picea excelsa.* It is demonstrated first of all by the position of the leaves, which are arranged in continuous spirals, and further by the cross sections of the fasciation at different points. They all show the vascular bundles and the pith arranged as a single, continuous mass, and not as a combination of a number of adjacent rings, which would have been the case had the fasciation resulted through the union of various originally distinct branches.

For the sake of convenience in discussion, the causes of malformations in general and fasciation in particular will be considered under four heads: (1) Mechanical action, brought about by the elements, man or other vertebrates; (2) cases where no injury can be traced; (3) the action of fungi; and (4) the action of insects.

Traumatisms appear, in the majority of cases, to be the inciting causes of the appearance of teratological characters. Numerous instances of this are to be found throughout our literature. Blarighem[25] found that in the case of the pansy, *Viola tricolor* var. *maxima,* it was caused by an accidental crushing of a young shoot. Similarly, he has been able to constatate[26] that in clover fields which had been mowed twice, the number of individuals of red clover, *Trifolium pratense,* bearing 4–5-foliate leaves, was from 12 to 37 per hundred, while in fields which never had been cut, but 5 to 8 such plants were found per thousand. Sainfoin, *Onobrychis sativa,* under the same conditions, produced in its pinnate leaf, leaflets grouped in threes and fours. Plants of the ox-eye daisy, *Leucanthemum*

[24] *Ibid.,* 333.

[25] Blarighem, L. Production par traumatisme d'anomalies florales dont certaines sont héréditaires. *Bull. Mus. d'Hist. Nat.,* 10: 399, 1904.

[26] Blarighem, L. Anomalies héréditaires provoqués par les traumatismes. *Compt. Rend. Acad. Sc.,* 140: 378, 1905.

vulgare (*Chrysanthemum leucanthemum*), of which the stems had been cut, bore heads on which at least a part of the ligulate flowers had been changed to tubular flowers, as well as heads, which in the axils of the bracts, bore secondary ligulate florets. Life[27] mentions the case of a plant of *Ambrosia artemisiæfolia* which, having been run over by a wagon and badly injured in consequence, bore both staminate and pistillate flowers in an abnormal condition. A hedge composed of plants of *Cereus margi-*

"Rosa de Organo"—*Cereus marginatus.*

natus, which, under the name Organo, is largely used as a hedge plant in Mexico, which was partly injured, probably because of securing cuttings for planting, shows numerous fasciations.[28] Klebs[29] mentions the observations of Krasan, who noted fasciation caused by a loss of leaves through the action of june bugs or spring frosts.

[27] Life, A. C. An Abnormal Ambrosia. *Bot. Gaz.*, 38: 383, 1904.

[28] A photograph, by Professor Frederick Starr (reproduced here), illustrating a large portion of a hedge thus fasciated, and a cast of one of the branches, are in the herbarium of the Missouri Botanical Garden. See also *Trans. Acad. Sc. St. Louis,* 9: xx, 1899.

[29] Klebs, G. Ueber künstliche Metamorphosen. *Abh. naturf. Gesell. Halle,* 25: 134, 1903–1906.

It is but natural to suppose that if accidental mechanical injury can produce abnormalities, the same can be produced experimentally through similar action. Again, numerous cases are on record. The first instance known is probably the experiment of Sachs,[30] who, amputating the main stem of bean seedlings just above the cotyledons, was able to bring about fasciation of the shoots produced from the buds in the axils of the cotyledons. A fasciation of *Ibervillea sonoræ* at the New York Botanical Garden, referred to in *Torreya*,[31] is understood to have been artificially caused by intentional slight injury of the growing tip. Blarighem[32] was able to cause fasciation of shoots of *Viola tricolor* var. *maxima* by crushing the young stems. Lopriore,[33] incited by the experiments of Sachs, cut the root tips of seedlings of *Vicia Faba* and obtained fasciated roots in a large number of cases, as well as malformations of other parts of the plant.

But apparently a fasciation is not necessarily a consequence of mutilation. Goebel[34] mentions fasciations in suckers and watersprouts. These are so common that they probably have come within every one's notice. Fasciations also frequently occur in plants the seedlings of which were abnormal in having a larger number of cotyledons than usual.[35] It has been shown[36] that under proper conditions of moisture and food, plants will frequently fasciate, though adjacent plants may remain normal. Such cases have generally been ascribed to peculiar conditions of nutrition.

[30] Sachs, J. Physiologische Versuche über die Keimung der Schminkbohne (*Phaseolus multiflorus*). *Sitzungsber. d. k. k. Akad. d. Wiss. in Wien*, 37: 57, 1859.

[31] Knox, Alice A. Fasciations in *Drosera, Ibervillea,* and *Cecropia. Torreya,* 7[5]: 102.

[32] *Loc. cit.*

[33] Lopriore, G. Verbänderung infolge des Köpfens. *Ber. d. d. Bot. Ges.,* 22: 304, 1904.

[34] Goebel, K. Organographie der Pflanzen, 164, 1898–1901.

[35] De Vries, Hugo. Eine Methode, Zwangsdrehungen aufzusuchen. *Ber. d. d. Bot. Ges.,* 12[2]: 25, 1894.

[36] 17th Ann. Rep. Missouri Botanical Garden, 147, 1906.

That parasitic fungi are able to produce an alteration of form in plants has long been known. One of the most familiar abnormal growths from such a cause is what is commonly termed a witch's broom, so often observed on evergreens. It is due to the action of species of Exoascus and Æcidum, which induce the formation of a large number of adventitious buds within a comparatively short area of the stem or branch, which give rise to a corresponding number of short, thickened twigs. In the silver fir, *Abies pectinata,* witches brooms are produced by *Æcidium elatinum.*[37] Frequently galls are produced by fungi, affecting either roots, stems or leaves, but no cases are on record where a fungus was shown to be the cause of fasciation. This is different where gall-insects are concerned. Here some cases have been traced directly to gall-insects[38] as the cause.

Galls, otherwise known as cecidia, and distinguished according to their origin into zoo- and phytocecidia, are among the most interesting of the abnormal forms which from time to time make their appearance as excrescences of widely varying shape, color and structure. Recognized by Pliny, some were even in those early days used in medicine because of their astringent properties. To-day, a number of them, especially some occurring on certain species of Quercus, Pistacia, Rhus and Tamarix, are of economic value[39] on account of their tannin content, and a gall produced by *Cynips tinctoria* upon branches of the dyer's oak, *Quercus lusitanica* (*Q. infectoria*), found in the countries bordering the Mediterranean and in the Orient, is official in the U. S. Pharmacopœia. Members of widely different orders of insects may be the cause of the

[37] Kerner, A., and Oliver, F. W. The Natural History of Plants, 2: 527, London, 1894–5.

[38] Though gall insects only are discussed here it does not follow that larvæ of other insects may not be the cause of fasciation. The relation between fasciation in species of Œnothera and the larvæ of a small moth, Mompha, is discussed in a very interesting, well illustrated paper by Knox, *The Plant World,* 10[7]: 145.

[39] Wiesner, J. Die Rohstoffe des Pflanzenreiches, 1: 674, Leipzig, 1900.

production of a gall. Among the Arachnida, many of the mites do so, some species causing serious injuries; for instance, the pear leaf blister mite, *Eriophyes pyri*, and *E. oleivorus*, which causes the so-called "russet" oranges.[40]

To the Hemiptera, of which the plant-lice, Aphididæ, are best known, belongs the dreaded *Phylloxera vastatrix*, which some thirty years ago so seriously crippled the vineyards of France. It forms galls on both the leaves and the roots. The Diptera, to one of the families of which our common house fly belongs, yield the Cecidomyidæ. One of these very small insects is the cause of the goldenrod rose. Neither the Lepidoptera nor the Coleoptera have many members which are the cause of gall formation. This is different as far as the Hymenoptera are concerned. A large number of species, especially those belonging to the Cynipidæ, are the cause of the formation of some of the largest, most strikingly colored galls, of which those occurring on oaks (Cynips) and roses (Rhodites) are probably the most familiar.

In some cases the causation of fasciations has been ascribed to gall-forming animals. Kerner[41] speaks of the fasciations of the ash, *Fraxinus excelsior* and *F. ornus*, caused by a mite, Phytoptus (Eriophyes). De Vries[42] mentions a stem of *Hieracium vulgatum* attacked by *Aulax Hieracii* which was normal below the gall, but above it was fasciated. Not only fasciations, but numerous other monstrosities have been brought into relation with gall insects. Treub[43] observed virescence caused by the same insect. Nalepa[44] mentions *Phytoptus anthocoptes* as the cause of virescence of flowers, thickening of the capita and frequent secondary formation of capitula on *Cirsium*

[40] Cook, M. T. Insect galls of Indiana. Indiana Dep. of Geol. and Nat. Res., 29th Annual Report, 801, 1904.

[41] *Ibid.*, 2: 549.

[42] Mutationstheorie, 1: 291.

[43] Treub, M. Notice sur l'aigrette des Composées a propos d'une monstruosité de l'*Hieracium umbellatum*. *Arch. Neérl. d. sc. phys. et nat.*, 8: 1.

[44] Nalepa, A. Neue Arten der Gattung *Phytoptus* und *Cecidophyes*. *Denkschr. d. k. Acad. d. Wiss.*, 59: 525, 1892.

arvense, P. cladophthirus as the cause of gray-hirsute malformations of the shoots of *Solanum Dulcamara,* and *P. genistæ* as the cause of malformations of the tips of the shoots and abnormal hirsuteness of the buds of *Genista pilosa* and *Sarothamnus scoparius.* The virescence of the inflorescence of different species of Arabis, due to Aphides, was studied by Peyritsch.[45] De Vries[46] ascribes an epidemic of virescence among the plants in his experimental garden to an original infection caused by Phytoptus, though he was unable to demonstrate the presence of the mite. Finally Molliard[47] investigated the influence of fungi and insects causing floral cecidia upon the reproductive cells.

From the above it will be gathered that there exists a very definite relation between malformation in plants and gall-insects. For this reason a large number of strikingly abnormal plants of the horse-weed, *Erigeron canadensis,* growing within a narrowly circumscribed area in the immediate vicinity of St. Louis, Mo., attracted immediate attention and awakened considerable interest. Being found in January, nothing but the dried parts remained, which made observation easier. All of the plants were abnormal. Among them two distinct types could be distinguished. These types agreed in one particular. From the ground to a place 2½–3 feet above the soil, the plants were normal. It was above this point that the abnormality presented itself. In the first type, when the plant had reached a height of from 2½–3 feet above the ground it had evidently experienced a check. The main stem terminated here in a very much dried-up shoot but an inch or less in length, showing that it never had an opportunity to perfect its woody tissue. Just below this point numerous small side shoots occurred. These side

[45] Peyritsch, J. Zur Ætiologie der Chloranthien einiger Arabis Arten. *Jahr. f. Wiss. Bot.,* 13: 1, 1882.

[46] De Vries, Hugo. Een epidemie van vergroeningen. *Bot. Jaarb. Dodonæa,* 8: 66, 1896.

[47] Molliard, M. Recherches sur les Cécidies Florales. *Ann. d. Sc. nat. bot.,* 8. Sér., 1: 67, 1895.

CECIDOMYIAN DEFORMITIES OF *Erigeron*.

shoots had an average length of from 1½–2 feet, and, issuing within a space of 3 inches from the atrophied tip, gave the dried plant a peculiar broom-like appearance. Upon them, usually immediately at the base, frequently within 2 or 3 inches from the base and sometimes at a distance of one foot from the base of the side shoot, occurred elongated swellings, from ½–¾ inch long and increasing the thickness of the stem to three times its normal size. These also occurred on stems of the second type, which bore fasciations. Each of the swellings contained a single orange-colored larva, which Dr. M. T. Cook kindly determined as that of *Cecidomyia origeroni.* The species of Diptera, to which *Cecidomyia* belongs, lay their eggs on the surface of the plant, and the larvæ, after hatching, penetrate the tissues. In this they agree with the Arachnida and Hemiptera. The Hymenoptera puncture the tissues and deposit their eggs within the plant tissues. It has long been a question in exactly what manner the abnormal growth due to gall insects is caused. Some ascribe it to mere mechanical irritation on the part of the larvæ, others believe it to be due to a chemical stimulus emanating either from the parent insect, which, at least in some instances, deposits, along with the egg, a certain chemical substance, or from the young larvæ only.[48] The latter happens in the case of the gall caused by *Cecidomyia Poæ* upon *Poa nemoralis,*[49] and which brings about the formation of roots in places where normally they are never found. But when *Nematus Capreæ* makes a wound in the leaf tissue for the purpose of depositing an egg, a gall develops, whether an egg is laid or not. Even when the former has taken place, though the egg be subsequently destroyed, the gall develops just the same, though never attaining full size. For that matter, mere mechanical irritation, *i. e.,* the killing of one or a few cells at the

[48] Beyerinck, M. W. Beobachtungen über die ersten Entwickelungsphasen einiger Cynipidengallen, 177. *Veröffentlicht d. d. k. Acad. d. Wiss. zu Amsterdam,* 1882.

[49] Beyerinck, M. W. Die Galle von *Cecidomyia Poæ* an *Poa nemoralis. Bot. Zeit.,* 43[20]: 304, 1885.

side of an organ, may result in the malformation of the adult organ, and, according to Ward,[50] may be proved experimentally by aid of a needle. But the assumption of a mere mechanical injury is not sufficient to account for the presence and shape of galls. The same insect, on different hosts, may produce different galls. Again, two distinct species of gall-insects produce very different galls on the same plant or even on the same leaf. Further, experiments to bring about artificially the formation of galls through the injection of different chemicals, have thus far proved unsuccessful.[51]

Among plants of *Erigeron canadensis* fasciation appears to be quite common.[52] When, however, among the plants of this fleabane infected by the Cecidomyia a large number, at least 10 per cent., were found to be fasciated, it was but natural to attempt to bring the two phenomena into relation. In some of these fasciated plants the fasciation begins within two feet of the ground; in others, and these form the majority, the fasciation began from 2½–3 feet above the soil surface and above the point where the galls occurred on the main stem. But while the non-fasciated plants showed a large number of long side shoots, developed at the expense of the main stem, the fasciated plants did not differ materially from normal plants in this regard. A large number of short side shoots bearing flowers were produced on a fasciated main stem. The most plausible explanation is that in the former case the growth of the main stem was inhibited absolutely and that all the strength went to form side shoots, while in the latter case the growing point was not affected sufficiently to dry up. Instead, growth was stimulated. Whether the action of the galls was of a mechanical or chemical nature, though of great interest in other cases, is of comparatively little importance here, and for the following reasons:

[50] Ward, H. Marshall. Disease in Plants, 131, London, 1901.

[51] Küstenmacher, M. Beiträge zur Kenntnis der Gallenbildungen mit Berücksichtigung des Gerbstoffes. *Jahrb. f. wiss. Bot.*, 26: 82, 1894.

[52] Penzig, *loc. cit.*

It has been conceded generally that fasciations are due to changed conditions of nutrition. Nestler, de Vries, Goebel, Sorauer and many others agree that they are induced either through an increase of nutrition of the entire plant or of that of certain shoots through the removal of others. In other words, it is due to a change of the chemical and physical conditions within the cell. The influence of chemical substances upon plant and animal cells has been widely studied. Among the best known are the experiments of Johannsen[53] in which lilac bushes and other flowering shrubs, of which we see the branches in the florist's windows in early spring, under proper conditions of moisture and temperature, were for a certain length of time exposed to the action of ether or chloroform, after which they bloomed several months earlier than normally would have been the case. Loeb's experiments on the cleavage of unfertilized eggs of the sea urchin, after having been treated with magnesium chloride, are too well known to make it necessary to go into detail. The same thing is true for his studies on the influence of the lack of oxygen and resultant modification in the cleavage of eggs of Echinodermata. Migula's experiments on the influence of dilute acid solutions on algal cells, Richards' work on the development of fungi under the influence of chemical stimuli, and especially the work of Sabline on the influence of external agents on the roots of *Vicia Faba* show that external influences may bring about profound nuclear changes. Still better, this is brought out by the injection experiments of MacDougal,[54] who was able to produce new species through the injection of dilute salt solutions into the capsules of evening primroses. And in the case of hyphæ of many of the Chytridiaceæ, which bring about abnormal cell divisions in the tissues of the host plant, the protoplasm of

[53] Johannsen, W. Das Aetherverfahren beim Frühtreiben, 2e Aufl., Jena 1907.

[54] MacDougal, D. T., A. C. Vail and G. H. Shull. Mutations, Variations and Relationships of Œnotheras. Carnegie Institution of Washington Publication, No. 81, 1907.

the parasite never comes in direct contact with that of the host. Yet their influence extends to cells at some distance from the point of infection. Even where the hyphæ do not actually enter the cell, a stimulation to abnormal growth often takes place. Experimentally mere mechanical action has brought about profound changes. Molliard was able to induce the formation of double flowers through mechanical irritation.

That the action of galls is of a chemical nature is well shown by Molliard,[55] who describes and figures profound nuclear changes preceding the hypertrophy of *Geranium sanguineum* attacked by *Phytoptus Geranii.*

If fasciations, which are due directly to chemical changes within the cells, may be inherited, then why not galls? But acorns from an oak covered by galls produce normal plants only. Still, one might expect galls to be inherited in preference to fasciations. Does not de Vries[56] say: "It is clear that the beautiful, highly complex and judicious structure of the cynipid galls, with their food tissue, layers of stone cells, and the tannin-bearing, loose, outer parenchyma, in thickness adapted to the egg apparatus of the parasites and inquilinæ, can not be brought about by a mere mechanical stimulus." Kerner goes so far as to say that it is within the limits of possibility that the first double flowers were caused by some gall.

There is no direct evidence of the inheritance of abnormalities brought about through the influence of gall insects or their larvæ. Fasciation, however, from whatever cause, may be inherited by a greater or less percentage of the offspring. We may then assume there must be a predisposition to the formation of fasciation in all plants which up to this time have been known to produce them. Probably this disposition is present in all other plants. The assumption of a mere excess of nutrition is not

[55] Molliard, M. Hypertrophie pathologique des cellules végétales. *Rev. gén. bot.*, 9me: 33, 1897.

[56] Mutationstheorie, 1: 290.

sufficient to explain the inheritance of the character. It is necessary to assume a corresponding and very definite change in the bearers of the hereditary characters. Just how these bearers are constituted or what name is given them is entirely immaterial. It is probable that they are of an exceedingly complex nature. For purposes of illustration they may well be compared with the molecules of organic chemistry, or better still, as has already been done so felicitously, to many-sided prisms, which a very slight jar causes to assume a different position and which finds a corresponding external expression. Under predisposition to fasciation or the latency of the fasciated character should perhaps be understood a tendency on the part of the cell contents, and more particularly the chromatin, to undergo a certain definite change, retained during cell division, of either a chemical or physical nature, under certain conditions brought about by differences in nutrition. The change which causes fasciation is one of the easiest brought about, and hence fasciation is one of the abnormal characters most frequently met with. Though a mere theory, its general truth is supported by a number of instances. Mutations frequently repeat themselves. The identical sports originating from stock obtained from widely different sources and where the probability of a common origin in the remote past may safely be questioned, speak for themselves. The finding in two distinct places in Europe of plants of *Capsella heegeri* Solms, which differs from *C. bursa-pastoris* mainly in the shape of its capsules, is another instance. Mutations in a species are always the same, whatever their direction. They may be widely separated in time and space, but whenever they appear they are identical.

It has been said that fasciations are inherited because the seeds collected for purposes of propagation always were obtained from the abnormal stems. This appears to have happened in the majority of cases. Since, however, we never can know whether a fasciation is inherited

or makes its appearance for the first time,[57] numerous experiments should be undertaken with a view of eliminating "chance" through large numbers. Whether the seed of a bean in which a fasciated root has been produced artificially, gives rise to a fasciated plant, is an experiment worth trying. Likewise, it is an open question whether the seed borne on normal stems of a pansy in the main stem of which fasciation has been induced through crushing, will give rise to fasciated individuals. The spores of the Boston fern, *Nephrolepis exaltata bostoniensis,* give rise to plants the majority of which exhibit the peculiar cristate leaves. Yet here and there on the fronds sometimes will be found non-cristate leaflets. Will the spores borne on the latter give rise to the cristate form? These are experiments which any one with a little space and time at his command and a penchant for gardening, can readily undertake. To such, no small hope of reward is held out in a recent paper by Blaringhem,[58] who, as a result of mutilation, obtained entirely new and constant varieties.

[57] This is true even when it appears as a bud variation, for the character may have been latent in the parent plant. One can, therefore, not speak, in such a case, of an "acquired" character in the strictest sense.

[58] Blaringhem, L. Action des traumatismes sur la variation et l'héridité. *Compt. Rend. hebd. d. Séanc. et Mém. de la Soc. de Biol.*, 57^2: 456, 1905.

THE AGGREGATE ORIGINATION OF PARASITIC PLANTS

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In the January number of The Naturalist I gave a review of the known phenogamous parasites, in which was discussed the relation of the parasites to one another, and to other abnormal plants; and the relation of all of them to normal plants. The present article is devoted mainly to the question of the manner of origination of the parasites as such, which, it is assumed, was by abnormal aggregate mutation from normal phenogams.

Parasitism in the animal kingdom is perpetrated by low, upon higher, forms of life, the parasites belonging to families, orders and even to classes, which are widely different from any of those which include the hosts. Parasitism of low forms of vegetable life upon higher forms is also everywhere prevalent, such as that of fungoid cryptogams upon phenogams, but the cases now under consideration are those of parasitism of various kinds of phenogamous plants upon other phenogams. Evidence of this phylogenetic relationship of parasites and their hosts, even in extreme cases of parasitic deformation, is fortunately preserved in that part of the structure of the parasites which pertains to parturital reproduction. That is, the florescence and fruitage of the parasites have remained characteristically phenogamous, each parasitic species having preserved at least those floral and pericarpal structures which normally characterize the phenogamous families, as such. It is thus observable that, in the abnormal mutation which produced the parasites, the effect was chiefly confined to the somatic parts of the respective plants and to those parts which are concerned in blastemal reproduction; while the parts immediately concerned in systematic genesis by parturital

reproduction were, at most, only slightly disturbed. So distinctly are the systematic characters of normal phenogams retained in the florescence and fruitage of the parasites that one seems forced to the conclusion that, in the great systematic development of vegetal forms, they all became phenogams before they became parasites. The phenogamous parasites, therefore, not only do not belong to a separate and predatory class, as is the case with other parasites, but they are depraved members of the same class, and sometimes of the same family, with their hosts. Still, their depravity is only with reference to the habits and structure of normal plants, for they all have great adaptability to their peculiar conditions, and their vegetal vigor is quite as great as is that of normal plants.

It is a fact worthy of special attention in this connection that although all the various forms of phenogamous parasitism are accompanied by greater or less abnormality of structure, they are in certain respects subject to the systematic restrictions which pertain to normal plants. That is, each form of parasitism affects not merely certain individual members of a given species, but every member of it; and the systematic limits of that species are, for itself, the limits of its own peculiar form of parasitism. Moreover, that form of parasitism which characterizes each of the different groups is shared without variation by every member of the group regardless of the generic or family relationship which it may bear to other plants. The habits and other parasitic characters of those depraved phenogams are as distinctly and permanently heritable as are the stated specific, and other systematic, characters of the same, or of any other, species, and there is no known evidence that any form of phenogamous parasitism has been derived by transmutation from any other parasitic form. Known evidence tends to show that every case of such parasitism originated independently of all other cases, and by a mutative process which imposed permanent abnormal characters

upon normal plants. Those abnormal characters all became connate with the normal characters after the establishment of their heredity, but they never became systematically correlated with them.

The questions that here almost crowd themselves upon one's attention are, how have those wayward phenogams accomplished their departures from normal conditions, and what was their incentive for doing so? Doubtless in all cases the chief incentive to parasitism, after the operation of an unknown predeterminate cause, has been food-lust, the instinctive object of the plant being to procure its nourishment in an immediately available form. The following respective references to the seven groups of phenogamous parasites are necessary to the present subject, but they show how difficult it is to make any sufficient answer to the first of those questions.

In pursuance of the subject as just indicated it may be suggested that the members of group I, which prey upon the roots of other plants and are only partially parasitic, originally acquired their habit of underground pilfering by the accidental chafing together of the tender roots of closely-growing plants, which brought bared, new-formed cells into contact at the crossings of the roots. Vital union of the roots at those points, such as takes place in grafting, having resulted, the more vigorous plant became the parasite by withdrawing a portion of the partly elaborated food-sap from the weaker one. It is plain, however, that thousands of cases are constantly occurring of similar contact of growing roots which do not result in parasitism. Both the normal and abnormal characters are possessed by every individual plant of every species pertaining to group I, and they are thus, all to the same extent, distinguished from normal plants and from all other parasites. In no case is one of this simplest of the forms of phenogamous parasitism known to show any inclination to greater complexity, or to abandon its present restricted parasitic habit. The heredity of that habit is permanent, and no known fact suggests that

it originated by any slow process, such as is generally understood to be the case in natural selection.

The mistletoes, which represent group II, have reached the condition of complete parasitism with less structural and functional change than have any of the other recognized groups. In view of the fact that they produce their own chlorophyl, and that their structure is very nearly normal, one can not doubt that they were originally normal phenogams, growing from the soil, although they will not now grow there. As a family also, they are now quite distinct from all other families, and as a group of parasites they are so clearly separate from every other group that one can not doubt that they have reached their parasitic condition in an entirely different manner. Their departure from the life-habit of normal phenogams evidently consisted only of the transference of germination and epitropism from the soil to the bark of trees; while the epitropic structure and functions, including both parturital and blastemal reproduction remained normal. Unnatural and lacking in apparent incentive as has been that transference, it is believed to have been suddenly accomplished for the whole family, no trace of transitional stages of parasitism having been discovered for the species of either the Old World or the New. Although the mistletoes are so nearly normal in structure, their parasitism is as complete and heritable as is that of any of the other groups.

The European species, *Lathræa squamaria,* which has been chosen to represent group III, besides being distinct from all other known parasitic forms, is, in a peculiar manner, suggestive of the assumed suddenness with which changes from normal to parasitic conditions have occurred among phenogams. This species has five distinct abnormal habitudes, which are repeated in succession in every individual plant. Its germination is from an ordinary seed in surface soil, and it is developed as a normal plantlet from a normal embryo; but it soon abandons itself to a remarkably diversified life. First, it produces

sessile haustoria upon some of its early roots and becomes partly parasitic in the same manner as do the members of group I, the structure and habit of which it then closely resembles. Second, it resorts bodily and suddenly to underground life by burrowing into the soil, where it becomes an intricate mass, often very large, of blanched stems and branches. Third, it abandons its early roots with their sessile haustoria, develops new pediculate haustoria from its underground stem and branches and becomes completely parasitic. Fourth, it changes some of its numerous aborted leaves into ingenious traps with which it captures minute animal forms and adds them to its other ill-gotten subsistence. Fifth, almost suggestive of atonement for a groveling life, it provides for the normal germination of its offspring by sending above ground a few specialized branches which produce perfect flowers and seed and then die, while the underground parts live perennially. That series of changes of structure and habitude within the life-history of a single plant has no known parallel in the vegetable kingdom. The changes have no apparent relevancy with one another until the closing one of the series, parturital reproduction, restores the normal phenogamous condition for a new reproductive cycle and a new series of the abnormal changes. All these changes of structure and habitude are invariable in character and invariably heritable. So far as is now known they are confined to a single species, and the structure of no other known plant offers any suggestion of their gradual origination. In view of such facts as these, all of which have been attested by competent observers, one may reasonably believe that not only this form, but all the forms of phenogamous parasites, have originated suddenly.

Although groups I, II and III are, by their respective methods of parasitism, clearly distinct from one another and from normal plants, parasitism is not physically manifested in any of them until after germination is completed, because the embryo of every member of each of

those groups is of normal structure. Every member of the four remaining groups, however, begins life in an embryo which is simple and filiform and without cotyledons, radicle and plumule, although the flower in which it is produced is of normal phenogamous structure. Moreover, although the simple abnormal embryo is physically identical for each of the four groups just mentioned, the resulting forms of parasitism are too widely different for each group to suggest for them even a remote community of origin.

A remarkable fact concerning group IV is that the two genera which compose it, Cuscuta and Cassytha, belong to widely different families, namely, Convolvulaceæ and Lauraceæ, respectively, and that the respective genera prevail in distantly separated parts of the world. Both genera are endowed with a single parasitic impress which distinguishes and dominates them equally in both habitude and somatic structure. That impress also separates all the species and individual plants of the whole group from normal plants and from all other parasites. The habits of this group, as shown by our well-known dodders, are widely different from those of all the other parasitic groups. They are all annual plants and consequently the whole life history of each species is crowded into a single season, which is shortened by late spring germination and early frosts. Therefore all the characteristics of the whole group lie dormant in the simple filiform embryo of every dodder seed for more than half of each year; and yet every one of those characteristics is invariably heritable and constant. Difficult as it is to understand how every individual member of such a distinctly defined double group of annual plants could have assumed their abnormal characteristics either slowly or suddenly, and attained a world-wide distribution, it is still more difficult to understand how two such diverse genera could have assumed identical parasitic characters. It is almost superfluous to add that the habits and structure of no known plant offers any suggestion of a gradual origina-

tion of the parasitic characters of group IV, or of the manner of its world-wide distribution.

As is the case with the other groups which are herein mentioned, nothing is known of the pre-germinative history of the characteristics of group V. The members of this group belong to a noted family of parasitic genera, the Orobancheæ, of which the destructive broom-rapes are among the best known examples. They all begin life in a simple, filiform embryo, which is not only without differentiation into cotyledons, radicle and plumule, but which is also extremely abnormal in its method of germination. The members of group V, like those of group IV, are annuals. As regards the structure of the seed and embryo and the initial conditions of germination, the members of both groups are similar, but their results are extremely different. The germinating offshoot of the former springs upward, sending no root into the ground, but seizing upon the growing parts of its companion plants by its haustoria. The offshoot of the latter burrows downward and seeks a root-host, failing to find which it dies without producing any upward growth. Finding a root-host, a substituent plantlet is developed from their conjoined parts which rises above ground, producing flowers and seed. The physical structure of the embryo of both plants is identical, and both are abnormal. Immediately upon germination the great differences between the plants appear, but neither in those differences or in their common embryonal structure is there any suggestion of a community of origin with each other, or with any other plants.

A leading characteristic of all the forms of phenogamous parasitism is the permanence and heredity of their attributes. Increasing abnormality of structure and habit, however, is suggested, but not proved, by the members of group VI, which is represented by the Rafflesias and some closely related genera. The conception which one naturally forms of a phenogam that may have been the normal ancestor of these plants is one having root, stem,

branches, leaves, flowers and fruit. These plants have discarded most of those essential parts, none of them having more than a short stem besides the fertile flower; and the sessile species, which are numerous, retain only the flower. Such a conception would therefore carry with it the idea that those eliminations were consecutively effected until the lowest structural limit was reached; but neither their own structure nor that of any other known plants affords the least indication that any of these parasites reached their present condition by either selective gradation of successive steps. The Rafflesias, like the mistletoes, are parasitic upon trees, and the seeds of both will not germinate successfully upon the ground. One may well believe that when the mistletoes abandoned the soil and inflicted themselves upon trees they took with them, and retained, all that they then needed for their support. But when the Rafflesias made their similar change, as they are assumed to have done, they required from their hosts the fullest possible tribute. Apparently sure of receiving it, they discarded as no longer necessary the principal part of their own somatic and blastemal structures, the sessile species retaining only those parts which are concerned in parturital reproduction, namely, only the flower. Their success has been complete, for although they are rootless, stemless, branchless and leafless plants, and originate from a structureless embryo, they are among the most vigorous of vegetable forms, the flower of the largest species sometimes reaching a diameter of more than three feet. One cannot conceive of a wider departure from normal conditions than is presented by group VI, or of a more complete isolation of structure and habit from all other plants.

Group VII, which is represented by the Balanophoreæ, is remarkable for the comparatively large number of systematic genera which it embraces, some of which are so greatly differentiated from others as to deserve recognition as sub-families. Some are comparatively inconspicuous; some produce large, showy flowers, and some

bear an outward resemblance to fungi, to which early botanists referred them. The genera of this group are still further distinguished by the comparatively small number of species which represent them, the average number to the genus being less than three. Yet all the members of this remarkably diversified group are developed from a simple filiform embryo by a germination similar to that of the broom-rapes, and all are rigidly controlled by one invariable and heritable method of parasitism. It is almost superfluous to add that there are no known intermediate forms between the parasitic species of this group, or between them and normal phenogams.

A leading purpose in the foregoing remarks is to express the belief and present evidence that all the various methods, or forms, of phenogamous parasitism have originated suddenly by abnormal mutation from normal phenogams and that each form originated independently of all the others. One can not doubt that, whatever may be the determinate cause, all mutations of plants, whether normal or abnormal, originated in changes of molecular conditions within the germ cell. Usually, those molecular changes are of phylogenetic character, but there is no reason to doubt that the changes which gave origin to the various parasitic attributes were also of like molecular origin. That is, referring to the theory of intracellular pangenesis of de Vries, each of those attributes, as well as their associated abnormalities of structure, both somatic and embryonic, had its origin in abnormal pangenes. Admitting such a community of molecular origin, there appears to be no more reason to doubt the origination of parasites by aggregate mutation than to doubt normal aggregate mutation.

One who accepts without qualification the theory of the origin of species by natural selection is no more likely to favor this idea of the sudden origination of the great and diverse groups of parasites which have been referred to in preceding paragraphs than he would be to accept the theory of special creation of species,

belief in which was formerly universally held. But by those who have given due consideration to paleontological facts with regard to the evidently sudden introduction at various stages of geological time, not merely of species, but orders and classes of animals and plants;[1] to the great array of facts presented by Professor Hugo DeVries in support of his mutation theory;[2] to the cases of aggregate mutation of Lycopersicum which I have published from time to time as results of my personal observations;[3] and to like cases of aggregate mutation of *Gossypium* which have been observed by Dr. O. F. Cook,[4] the proposition that the different forms of phenogamous parasitism have been introduced separately and suddenly will not be hastily rejected. When the attention of one who holds the former of the two views referred to is called to the cases of evidently sudden introduction of animal and vegetable forms during geological time he usually replies by deploring the imperfection of the geological record, although he constantly depends upon it in the multitude of cases in which phylogenetic continuity is evident. And yet, there is no break in the geological record, which is more abrupt and differential than is that which exists between the distinguishing characters of the phenogamous parasites and the normal characters of every other phenogam now living contemporaneously with them.

Briefly reviewing the foregoing subject, we find as follows: (1) The parasites which have been discussed are

[1] I have discussed these questions in Report of the Smithsonian Institution for 1901, pp. 631–640; *Bulletin Torrey Botanical Club*, New York, Vol. 29, pp. 511–522; Album der Naatur, Haarlem, April, 1903, pp. 231–238; Natur und Schule, Berlin and Leipzig, III Band, pp. 248–253; and *Science*, New York, Vol. XXII, n. s., pp. 105–113.

[2] Die Mutationstheorie, Leipzig, 1901.

[3] *Science*, n. s., Vol. XIV, pp. 841–844; *ibid.*, Vol. XVII, pp. 76–78. New York *Independent*, Oct. 16, 1902; *Bull. Torrey Bot. Club*, Vol. 29, pp. 511–522; *The Popular Science Monthly*, Vol. LXVII, June, 1905, pp. 151–161.

[4] *Proc. Washington Acad. Sci.*, Vol. VIII, p. 265; *Science*, n. s., XXVII, p. 193.

known to be phenogamous by the character of their florescence and fruitage, but for this occasion they are classified by their parasitic differences only. They are divided into no less than seven distinct groups, or kinds, which differ in character from root pilfering by means of a few haustoria to dominant rapacity, extreme deformation of somatic and embryonal structure and aberrant methods of germination. (2) The method of parasitism of each group is shared equally by every member of it, whatever may be the systematic affinities of the respective members, and the method of each group is entirely unlike that of every other group. (3) All the parasitic habits and structures are severally and completely heritable, and always connate with systematic features of the species in which they occur, but they are never systematically correlated with them. (4) None of the seven forms of parasitism shows any tendency to return to normal conditions, to become more complex, or to change from one form to another. (5) The normal florescence and fruitage of the parasites is assumed to indicate that they were originally derived from normal phenogams; but no trace of intermediate stages between even the most extreme cases of parasitism and normal plants has been discovered. The geographical distribution of all the known kinds of phenogamous parasitism, except that of group III, is almost world-wide. In consideration of these, and many kindred, facts it is assumed that the phenogamous parasites originated as such by sudden and aggregate mutation from normal phenogams, similar to, but not identical with, the phylogenetic aggregate mutation that has been observed in Lycopersicum and Gossypium.

THE EVOLUTION OF THE TERTIARY MAMMALS, AND THE IMPORTANCE OF THEIR MIGRATIONS[1]

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NOTE.—These very interesting and important papers by Charles Depéret, Dean of the Faculty of Science, University of Lyons, France, have been especially revised by the author (to date, November, 1907) before translation. The translation is the work of Miss Johanna Kroeber, graduate student of Columbia University. Dr. Charles R. Eastman of Harvard University and Dr. W. D. Matthew of the American Museum have kindly revised the translation. The correlation of the Tertiary of the Old and New World is of such commanding interest to paleontologists, zoologists and geologists, that this contribution from one of the foremost paleontologists of the continent is especially welcome.

HENRY FAIRFIELD OSBORN.

March 3, 1908.

FIRST PAPER. EOCENE EPOCH

In a preceding contribution (*Comptes rendus,* 5 juin, 1905) upon the principles of evolution of the Tertiary mammals, I have enunciated the following general law: that when we attempt to establish the sequence of the forms which represent the evolution of a *natural phylum* we find ourselves, after tracing them backward through a geologic series of more or less length, almost always arrested by an impassable hiatus; this *apparent break* corresponds to the sudden appearance of the group under

[1] Extract from the *Comptes rendus des séances de l'Académie des Sciences,* t. CXLI, p. 702. (Séance du 6 novembre, 1905.) Translated by Johanna Kroeber.

consideration in the region of the globe which one is studying.

It is desirable to return to this general law of *faunal changes through migration* and to illustrate its interest more fully.

The importance of the migrations of terrestrial animals as correlated with great changes in the *paleogeography* of the continents, was fully recognized a century ago by Cuvier. The illustrious founder of paleontology had been justly impressed by the absence or rarity of forms of passage between the superposed fossil faunæ. Exaggerating somewhat, owing to the imperfect evidence before him, the consequences of this observed fact, Cuvier had deduced from it the renewal of faunæ *in toto* (after their destruction by *terrestrial cataclysms*) not by successive *creations,* as he is often accused of advocating, but by extensive *migrations* of animals foreign to the region. Since his time, many paleontologists, Wallace, Lydekker, Zittel, Schlosser, Gaudry, Osborn, Ameghino, etc., have given their attention to this subject and have reiterated its significance. It appears to me, however, that these contributions have been of too speculative a character, inadequately supported by precise data. It has resulted that the majority of the essays at the *genetic* or *structural phylogeny,* which have been attempted in various groups of fossil mammals, are defective, chiefly because their authors have almost always sought to find in place in the particular country which they inhabit the various evolutionary series of these groups.

No doubt there are great practical difficulties in refastening link to link the segments of the broken chain which forms the evolutionary series of each of the innumerable branches of the mammalia. Nevertheless, the obstacles are smoothed away by each new discovery; thus the recent disinterment of the Oligocene and Eocene of the Libyan desert, of the ancestors of the Proboscidea, the Mastodons and Dinotherium, which appear so suddenly in Europe at the beginning of the Miocene, and

whose origin has been until now an insoluble enigma, indicates the method we should follow, and the necessity for searching for the *centers of dispersion* of each branch.

A preliminary work at least is possible at our present stage of knowledge; it is to establish for each region whose paleontologic exploration is sufficiently advanced, the part which pertains to each of the two factors determining faunal changes: (1) *Evolution of the local fauna* (autochthonic evolution), (2) *Immigrations from a distant region.*

I shall attempt to analyze these facts for the Tertiary faunæ of Europe, where this distinction has never been established in a systematic manner.

I. *Thanetian* or *Lower Londinian* stage (deposits of la Fère, Cernay, Rilly, Châlons-sur-Vesle in France; of Erquelines in Belgium).

1. *Local Evolution.*—A single instance, *Neoplagiaulax* (Multituberculata), which may perhaps have been derived, in spite of the great gap of the Cretaceous, from *Plagiaulax* of the Purbeck, but may also have migrated from North America.

2. *Migrations of North American Origin.*—Introduction into Europe of several families of Creodonta: Oxyclænidæ (Procynictis = Chriacus), Arctocyonidæ (Conaspidotherium = Clænodon), Mesonychidæ (Dissacus); and of the Condylarthra (Euprotogonia).

3. Migrations of unknown origin of the Insectivora (Adapisoricidæ), of the (?) Artiodactyla (Pleuraspidotheriidæ), of the aberrant Primates of the group Plesiadapidæ, of the Perissodactyla (Hyracotheriidæ or Preequidæ), of the Amblypoda (Coryphodon).

II. *Sparnacian* or *Upper Londinian* stage (deposits of Soissons, Guny, Muirancourt, Saron near Ste Maxence, Laon, Upper Cernay, Meudon, Vaugirard, Sézanne, in France; Dulwich and Croyden (Woolwich beds) in England. Fauna unfortunately still very scanty.

1. *Local Evolution.*—Continuance of Amblypoda (Coryphodon, and of Hyracotheriidæ (? Pachynolophus).

2. *North American Migrations* of certain Creodonta (Pachyæna, Palæonictis).

III. *Lower Ypresian* stage (beds of the London Clay, Herne Bay, Kyson, Harwich, Isle of Sheppey, in England; beds of Pourcy near Reims in France). Fauna little different from that of the preceding stage.

1. *Local Evolution.*—Continuance of Amblypoda (Coryphodon), and of Hyracotheriidæ (Hyracotherium).

2. *Migration of North American Origin* of the Tillodontia (Platychærops = Esthonyx).

IV. *Upper Ypresian* stage (beds of Teredo-sands, Ay, Cuis, Chavot near Epernay).

1. *Local Evolution.*—Continuance of Insectivora (Adapisoriculus), of aberrant Primates (Plesiadapis), of Creodonta-Mesonychidæ (Hyænodictis = Dissacus), and of Hyracotheriidæ (Propachynolophus).

2. *Important Migrations, Probably of North American Origin,* of the mesodont Primates (Notharctidæ, genus Protoadapis), of the Rodentia-Pseudosciuridæ (Decticadapis), and Sciuridæ (Plesiarctomys), of Lophiodontidæ (parallel branches Lophiodon and Chasmotherium), of the Paridigitate Suillines (Protodichobune) and perhaps of Titanotheridæ (Brachydiastematotherium).

This horizon is marked by some important migrations and great changes in the mammalian fauna, in consequence of which the latter approximate more closely to the fauna of the middle, than to that of the lower Eocene.

V. *Lutetian* stage, two successive faunæ:

(*a*) *Lower* and *middle Lutetian* (beds of Argenton, of Bracklesham and part of the "terrain sidérolithique" of Egerkingen and of Lissieu).

Local evolution of Lophiodontidæ (Lophiodon, Chasmotherium), of Hyracotheriidæ (Pachynolophus, Propalæotherium) and of Dichobunidæ (Meniscodon, Dichobune).

(*b*) *Upper Lutetian* ("Calcaire grossier" beds of Paris: Nanterre, Vaugirard, Gentilly; Coucy, Dampleix; of Buschweiler, of Issel; les Matelles, St. Gily du Tesc;

the larger part of the "terrain sidérolithique" of Egerkingen and of Lissieu).

1. *Local Evolution.*—Continuance of Lophiodontidæ (Lophiodon, Chasmotherium), of Hyracotheriidæ (Pachynolophus, Propalæotherium, and intermediate forms leading to Lophiotherium), of Creodonta-Oxyclænidæ (Proviverra), of Rodentia-Sciuridæ (Plesiarctomys), of Dichobunidæ (Dichobune, Mouillacitherium), and of the mesodont Primates (Cænopithecus, ? Adapis).

2. *Important Migrations of Unknown Origin* of the Palæotheriidæ (appearing suddenly with their two branches Palæotherium and Plagiolophus), the Anchilophidæ (Anchilophus), the Suidæ (Chœromorus, Acotherulum), the Anthracotheriidæ (Catodontherium n. g., forerunner of Brachyodus), the Dacrytheridæ (Dacrytherium), the Xiphodontidæ (Xiphodontherium), the Dichodontidæ (Dichodon, Tetraselenodon, Haplomeryx), some Sciuridæ (Sciurus), the Talpidæ (Amphidozotherium), the Erinaceidæ (Neurogymnurus).

3. *North American Migrations* of the Hyænodontidæ and probably of the Lemuroidea-Anaptomorphidæ (Necrolemur).

VI. *Bartonian* stage (calcareous deposits of St. Ouen near Paris) of Sergy (Aisne), sandstones of Castrais (Lautrec, Mazou, Viviers, Montespien, etc.), of Robiac (Gard), "terrain sidérolithique" of Heidenheim and part of those of Mormont; very small part of the phosphorites of Quercy.

1. *Local Evolution.*—Continuance of Lophiodontidæ (last of Lophiodon and Chasmotherium), of Hyracotheriidæ (primitive representatives of Lophiotherium), of Palæotheriidæ (numerous parallel branches), of Anchilophidæ (Anchilophus), of Anthracotheriidæ (Catodontherium n. g.), of Suidæ (Chœromorus, Chœropotamus), of Xiphodontidæ (Xiphodontherium), of Creodonta (Hyænodon), of Sciuridæ (Plesiarctomys), of Adapidæ (Adapis).

2. *Migration, perhaps of North American Origin,* of the Chalicotheriidæ (Pernatherium).

VII. *Ludian* stage, two successive faunæ:

(*a*) *Lower Ludian* (deposits of Saint Hippolyte de Caton (Gard), of Hordwell (Isle of Wight), lower strata of the Gypse de Paris; part of the Quercy phosphorites.

1. *Local Evolution.*—Continuance of Palæotheriidæ, of Hyracotheriidæ (last of Lophiotherium), of Anchilophidæ, of Suidæ (Chœropotamus, Cebochœrus), of Dacrytheridæ (Dacrytherium), of Xiphodontidæ (Amphimeryx), of Dichodontidæ (last of Dichodon), of Anthracotheriidæ (Catodontherium), of Hyænodontidæ (Hyænodon, Quercytherium), of mesodont Primates (Adapis) and Anaptomorphidæ (Microchœrus).

2. No new migration known.

(*b*) *Upper Ludian* (Gypse de Montmartre, deposits of Gargas, of Mornoiron, of Villeneuve la Comptal; of the Bembridge beds and the Headon beds in England; part of the phosphorites.

1. *Local Evolution.*—Continuance of Palæotheriidæ, of Anchilophidæ (last of Anchilophus), of Xiphodontidæ (Amphimeryz, Xiphodon), of Dacrytheridæ (last of Dacrytherium), of Anthracotheriidæ (first representatives of Brachyodus, earliest Anthracotherium), of Suidæ (last of Acotherulum, Chœropotamus, and Cebochœrus), of Dichobunidæ (last of Dichobune), of Hyænodontidæ (Hyænodon, Pterodon), of Sciuridæ (Plesiarctomys, Sciurus), of Adapidæ (last of Adapis), of the Lemuroidea (last of Necrolemur).

2. *Migrations of Unknown Origin* of the Anoplotheridæ (Anoplotherium), of the Cænotheridæ (Oxacron = Hyœgulus), of the Canidæ (Cynodictis), of the Rodentia-Theridomyidæ (Theridomys), and Myoxidæ (Myoxus).

3. *American Migration* of the Marsupial Didelphyidæ (Peratherium).

(*To be continued.*)

ZOOLOGICAL PROGRESS[1]

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THE chase, the domestication of animals, and the practise of animal sacrifice in religious ceremonies were all customs of primitive man that led to an acquaintance with animal structure and habit long before human knowledge could be said to be organized. In the early steps of this organization, what we now know as zoology was a part of natural history, but in the specialization of modern times zoology has grown to the dignity of an independent science with numerous subsciences. In fact modern specialization has gone so far that concern has been frequently expressed lest the natural unity of science be entirely lost sight of; but, in sketching the outline of zoological progress, I hope to show you that, so far as zoology is concerned, this fear is unfounded.

Any outline of the course of zoological progress must be somewhat in the nature of an inventory of zoological possessions, and I can not do better in beginning this brief survey than to call your attention at once to the real materials of zoological research. These are the individual animals, which, as you well know, are not immensely diverse, but show certain agreements whereby they may be arranged in groups whose members have similarity of form and habit and show the remarkable trait of producing new individuals of like kind. These natural groups or species afford a basis for a descriptive inventory of the animal kingdom, and the attainment of such a complete description has been perhaps one of the most persistent motives to zoological work.

Progress in this undertaking is indicated by the increase in the number of species described at each succes-

[1] An address delivered at The College of the City of New York.

sive period. Aristotle, who is usually regarded as the father of natural history and who lived in the fourth century B. C., mentioned in his zoological treatises about 480 kinds of animals. Linnæus, in the tenth edition of his "Systema Naturæ," published in 1758, described 4,378 species. Günther estimated that in 1830 a total of 73,588 species had been reached and that in 1881 the number had mounted to 311,653. Sharp placed the total in 1896 at 386,000, and, judging from the rate of increase in the vertebrates and echinoderms, the total number of described species at present must be approximately 500,000. From these estimates, which include only living species, it must be clear that in the twenty-two centuries between Aristotle and Linnæus the number of species known to the naturalist had increased only ten-fold, while in less than a century and a half after Linnæus the increase had been over a hundred-fold.

This enormous increase has been the result of two processes: the actual discovery of new forms in nature and the subdivision of what was originally regarded as one species into two or more species. The actual discovery of new forms implies the gradual exhaustion of nature and the conclusion of this process will come when exploration can yield no more new species. That the naturalist even of to-day is far from this goal is only too well known and can be illustrated by the following instances.

All of you doubtless have seen a delicate pearly shell, chambered somewhat like a miniature nautilus, but with its whorls open. This shell, which is known as the Spirula, is found commonly on the shores of the tropical oceans and may even reach our more northern coasts. It is extremely fragile and hence it can not last long on a surf-beaten shore. Nevertheless it is sometimes so abundant on tropical beaches as to form veritable windrows. Each shell is the life product of a single Spirula animal, which, so far as one can judge from the abundance of shells, must be a common inhabitant of the tropical seas. And yet, aside from fragments, the Spirula animals thus

far obtained number only six. The first was collected in New Zealand and dissected by Sir Richard Owen. The second, for which no locality is known, was purchased by the British Museum from a dealer and dissected also by Owen. The third was collected near Port Jackson, Australia, and is now preserved in the Sydney Museum. The fourth was dredged near New Guinea by the "Challenger" and was studied by Huxley and Pelseneer. The fifth was taken by the dredge in the West Indies by the United States steamer "Blake," and the sixth was caught near Sumatra in a deep-sea net by the German expedition on the "Valdivia." If an animal as common as the Spirula must be, is known only by some six specimens, what a host of rare and undescribed species the ocean must contain.

Not only are the ocean basins treasure stores of undescribed species, but the land areas are also far from exhausted. It would seem fair to have presumed that of the terrestrial quadrupeds certainly all the larger and more striking species had been described, and yet, since the opening of the new century, a large cloven-hoofed mammal in general appearance somewhat between a donkey and a giraffe has been discovered in the Semliki forests of central Africa. This remarkable mammal was sought for in 1900, at first unsuccessfully, by Sir Harry Johnston, who finally succeeded in obtaining a skin and a skull from which the animal was described by Lankester in 1902. The natives call it okapi and report it by no means rare, and yet it remained almost to the present time without being known to science. But the naturalist is not obliged to search the deep sea or to journey to central Africa for new species. There is hardly an order of insects that could not be enriched with new forms by a season's collecting even within the limits of New York City, and it must therefore be evident that the half-million of species now described is only the beginning in the inventory of nature's stores.

In addition to the discovery of new species in nature,

the process of splitting what was assumed by the older zoologists to be a valid species into two or more new ones has also considerably increased the number of described forms. This practise, though sometimes questionable, is at least illuminating, for it raises at once the fundamental question of what constitutes a species. In the days of Linnæus when special creation was more generally adhered to than now, it was comparatively easy to meet this question by the statement that a species is the aggregate of individuals represented by the originally created pair or stock and their descendants; but, with the acceptance of the evolutionary idea, this reply no longer sufficed. From the evolutionary standpoint every species has had a history and this history has been clearly one of change whereby the aggregate of more or less similar individuals at one time representing the species gave rise to the self-perpetuating stock whose more remote members evolved in one or more directions new features, so that the species either as a whole assumed new characteristics or split into two or more subordinate groups, each having its own special features and being destined eventually to become as well circumscribed from its next of kin as the original stock was at the outset. With this process in mind it is fair to expect that nature would be found to embrace many aggregates of individuals which would represent species at all steps of differentiation, and whether the individuals of a given aggregate had come to differ sufficiently among themselves to constitute a new species or not would depend entirely on the judgment of the naturalist who described them. It is thus clear that we can not expect any fundamental characteristic by which a new species can be definitely determined, for it is obvious that the transformation of species is a more or less continuous process in which the degree of separation whereby the new species will be established is somewhat arbitrarily determined by each describer. Hence the idea of species rests upon an artificial basis, and, if the describer's measure of specific difference diminishes with the progress of

time, it is perfectly legitimate to subdivide previously described single species into smaller aggregates to be denominated new species.

Where this movement will lead to is not easy to foretell. It was hoped that the statistical methods of biometric work would make possible a solution of some of the difficulties in defining species, but, while these methods enable the investigator to discover and express differences between large groups of individuals vastly more accurately than the old methods of simple inspection and rough mental estimate did, they do not settle what characters or how many such shall be used in defining a species or what degree of difference must be arrived at before a given aggregate may be divided into two or more species. Nor does the recent proposition of de Vries come nearer to solving the problem. According to this investigator real species can be defined by a certain combination of characters which vary not in a continuous way but by leaps. These discontinuous variations constitute differences that may be as distinct as the differences between chemical elements; and any real or elementary species, as de Vries designates it, is distinguished by one or more of these elementary characters. Such elementary species, though open to variation, are cut off absolutely in their specific characters from other such species by a gulf that is never bridged by intermediate forms. Hence they ought to be as easily and distinctly describable as chemical compounds or even chemical elements. These elementary species, which have been for the most part heretofore ignored or passed over simply as races, etc., are the real units of systematic zoology and are much more numerous than the ordinary or Linnæan species. In fact, each Linnæan species probably consists of many elementary species and consequently the acceptance of this proposition would multiply the number of described species many times. But the difficulty with this proposal is to be found in the fact that an inspection of the so-called elementary characters shows them to be not so

stable as de Vries assumed. In some characters, like coat colors, fixity is more or less realized; but in other features, particularly dimensional ones, such an amount of variation is shown that the resulting forms necessitate the same artificial methods of separation as those to which the older systematists were obliged to resort. From a radical standpoint there seems to be no escape from the view that a species is at best an imperfectly definable aggregate of more or less similar individuals and that this conception rests upon an artificial basis.

Although the idea of species must be admitted to be artificial rather than natural, its immense practical importance is not to be lost sight of; for, as a tool in the hands of the working zoologist, it is absolutely indispensable. Moreover, the arrangement of species into related groups and the development thereby of a system of classification has led to views on animal phylogeny of the utmost significance. That living animals range from the relatively simple unicellular protozoans to the immensely complex vertebrates suggests at once that the modern faunas include not only the latest products of animal evolution but many remnants of the remote past. This state of affairs is a continual temptation to picture the past history of the animal kingdom in terms of modern forms and to assume, for instance, that the protozoans of to-day are like the primitive protozoans from which the higher animals have been derived. This attitude leads to the discussion of the so-called affinities of the modern groups, a practise that in my opinion is open to the objection of attempting to make parents and grandparents out of brothers and sisters. How futile this practise is can be seen in such a group as the reptiles. You are doubtless aware that the modern reptiles are included in four orders: the chelonians, or turtles; the crocodilia; the rhynchocephalia, represented by a lizard-like reptile from New Zealand; and the squamata, or lizards and snakes. You are probably not so well aware that the class of reptiles also includes five other orders, all fossil, among

which are to be found some of most specialized and prodigious land and water animals known. No possible consideration of the recent orders of reptiles would ever lead one to suspect the remarkable nature of these ancient forms, and the so-called affinities of the recent orders become meaningless in the light of the true ancestral relations as seen in the past history of the group as a whole. Tempting as the field of speculative phylogeny is, its results can never be of much value till they receive the endorsement of actual history as traced in fossil ancestry. In this connection I can not do better than quote a short passage from Huxley, who, as you well know, was an ardent student of fossil as well as living animals. In his essay on "The Advance of Science" he says:

> A classification which shall represent the process of ancestral evolution is, in fact, the end which the labors of the philosophical taxonomist must keep in view. But it is an end which cannot be attained until the progress of palæontology has given us far more insight than we yet possess into the historical facts of the case.

It is plain that the history of the animal kingdom is to be sought for not through ingenious speculations on the recent groups of animals, but by the persistent and patient exploration of the fossil-bearing rocks.

Although the study of animal genealogy, as outlined by fossil remains, is a relatively novel field, it has already yielded certain general results worthy of careful attention. It is customary at present to group all species of animals under some ten or twelve main divisions or phyla of the animal kingdom. These phyla have doubtless been evolved from some common group of animals in the remote past, and consequently, in tracing back their history as represented by fossil forms, it is not unreasonable to expect that their lines would gradually converge toward this common ancestral stock. In some instances, like the flat-worms, the phylum is known only through its modern representatives, and these representatives are of such consistency that it is not surprising that none of these animals have been preserved in the fossil state. But,

aside from cases of this kind, all phyla that might be represented by fossils are, as a matter of fact, so represented; and the remarkable feature of this representation is that it does not show a convergence toward a common stock, but the phyla as such were as distinct in these early times as they are to-day. This state of affairs, which at first sight seems contrary to the evolutionary idea, is due in all probability to a universal destruction by extensive rock metamorphosis of the earliest of animal remains, and we are therefore probably correct in concluding that fossils at best give us only the later chapters in the evolution of the animal kingdom. Within a phylum the main lines of descent can sometimes be clearly discerned, but between phyla there are no absolutely certain connections, nor is there as a matter of fact a single completely extinct phylum known. These facts lead us to see that for an immensely long period the main divisions of the animal kingdom have been as they are at present and that the genetic connections of the phyla, which would be discernible with certainty only through their fossil remains, are, in consequence of the absence of these, probably absolutely and irrecoverably lost. Even the important suggestions that embryology has yielded as to the phylogenetic relations of the chief animal groups must remain forever hypotheses because of this irreparable blotting out of past records.

Although the systematic zoologist may look upon the animal kingdom as composed of imperfectly definable aggregates of individuals whose relations in the remote past are irretrievably lost but whose numbers are such as to occupy his labors for many years to come, his arrival at this conception has been over a course that has brought to view such a multitude of new prospects that the real extent of zoology is only now beginning to be dimly seen. These more recently acquired territories, which are now being cultivated with a vigor no less than that bestowed in past times almost exclusively on systematic zoology, must now be looked into. It is somewhat difficult for us

to conceive of the state of mind of the zoologist of a century ago so far as his conception of the structure of animals is concerned. To him they consisted of organs composed of a variety of unrelated substances, such as muscle, membrane, bone, fat, blood, etc., which constituted the elementary materials of the animal body. It was therefore a great step forward when Schwann showed in 1839 that animals, like plants, were composed of structural units or cells whose physiological significance, as Brücke afterwards pointed out, entitled them to the name of elementary organisms. Many lower animals, belonging to what are now called the Protozoa, proved to be single cells, while the higher animals in all cases were found to be multicellular. The number of cells entering into the formation of the body of one of these higher animals is truly enormous. It is impossible to get reliable statements for these numbers in any single complex animal, but a recent careful estimate of the number of ganglion cells in the human cerebral cortex places the total at 9,200,000. As this enormous number of cells would occupy less than a cubic inch of space, one can form some rude conception of the prodigious number in the whole human body.

It is a remarkable fact that almost all cells, whether they are whole single animals or only parts of animals, are of small size. There seems to be something about the organization of a cell which ordinarily prevents it from enlarging much beyond microscopic proportions. The essential parts of a cell are its nucleus and the surrounding cytoplasm, and the continued activity of the cytoplasm is known to be dependent upon the presence and integrity of the nucleus. Such being the case it would seem as though the nucleus could administer to only a limited volume of cytoplasm and thus restricts the size of the cell. Apparently, however, this relation is one of volume and not of distance from the nucleus, for the cytoplasm of a ganglion cell may be drawn out into a most delicate nerve-fiber process that may reach half the length of the human body.

The arrangement of the cells in the body of a multicellular animal is not, as in most plants, of a more or less promiscuous kind, but conforms to certain fundamental principles. Among these probably the most important is one that depends upon the fact that animals assimilate solid food. To carry out this operation they possess almost universally a digestive cavity into which this solid food is carried and there rendered soluble. The only multicellular animals that do not possess a digestive cavity are certain parasites, like the tapeworm, whose modes of life are such as to make digestive organs superfluous. In the simpler multicellular forms, the coral animals, etc., the whole animal is sac-like in structure and may be briefly described as an animated stomach. Not only is this state characteristic of such primitive forms, but in the development of almost every multicellular animal known, the first organ to be formed is the digestive organ. This is brought about in that the cells, which are destined for the future animal's body, become arranged in the form of a two-layered sac in which the inner layer or entoderm bounds the digestive space and the outer one or ectoderm acts as a protective covering. Both layers develop a certain amount of muscular tissue and this is brought into action through external stimuli that from the nature of the case are received usually by the ectoderm. Hence this layer becomes the seat of those changes which in the higher animals eventually shape themselves in the sensory and nervous organization of these forms, while the entoderm is concerned with the digestive functions. Between these two layers there develops in all the higher multicellular animals a third layer, the mesoderm, which, as has been intimated, is primarily muscular in character but may also give rise to the internal skeleton, circulatory system, and other related sets of organs. Thus the body of a multicellular animal is composed of definite layers or masses of cells, chiefly three in number, with which special functions or modes of activity have become firmly associated.

Although these cell layers as such retain their limits in a most striking and clear way in the bodies of the higher animals, they must not be thought of as independent or in any sense isolated in their development. Their mutual relations are often of a most intimate kind and in the course of their development these relations tend rather to become more firmly consolidated than the reverse. This condition is well illustrated by the growth of the neuromuscular mechanism in animals, a growth that can be traced step by step through the multicellular forms till it finally shapes itself into the complex machinery whereby the animal reflexes are carried out.

The first step in this process is seen in the sponges, which in some respects are the simplest of the multicellular animals. As is well known, these animals are quite as sluggishly responsive to stimulation as plants are. A long and unsuccessful search for their nervous organs has ended in the belief that they possess no such structures. Some of their cells, particularly in the neighborhood of their numerous pores, are elongated or even fibrous and are apparently contractile enough to serve as a means of closing these openings. It is highly probable that these contractile cells, which may be regarded as primitive muscle cells, are brought into action by some stimulus directly applied to them, such as dissolved materials in the sea-water, etc. We are so accustomed to think of muscle as controlled by nerve that independent action of this kind seems wholly anomalous. And yet it must not be forgotten that muscle can be made to contract by the direct application of a stimulus and that even in the higher animals under natural conditions this may occur. Steinach has shown that when bright light is thrown on the eye of a fish or an amphibian the pupil will contract even after all vestiges of nervous connections have been destroyed, and he believes this to be due to the direct stimulation of the muscle fibers by light. This case supports the opinion that in sponges the contractile tissue responds to direct stimulation, and in my opinion the

sponge represents the first step in the differentiation of the neuro-muscular mechanism, a step in which the primary and fundamental character of muscle is disclosed in that this is the only constituent present. This self-sufficiency of muscle is also made evident in the rhythmic beat of the embryonic chick heart before nervous differentiation has taken place.

In the sponges the primitive muscle cells lie either in the ectoderm or the subjacent mesoderm. In the coral animals, the jellyfishes, and their allies, the muscle cells occur in the deeper parts of the ectoderm and entoderm, a position where a forming mesoderm might be expected. It is usually stated that in the higher animals the muscles are derived from the mesoderm, and in individual development this is true, but from a phylogenetic standpoint I believe the reverse to be the case, namely, that the mesoderm has come from muscle and that the first step in the real origin of this layer is indicated in the migration of the muscular tissue of the cœlenterates or other like forms from the ectoderm or entoderm into the region between these two layers. This operation, which involves both layers in many of the lower animals, is usually limited in the higher forms to the entoderm, probably because this layer is the one which by reason of its proximity to the digestive cavity can best supply material for future growth. But, however this may be, it seems to me probable that the mesoderm has had its origin in the process of muscle formation, a process that is seen in its incipiency in the cœlenterates. That the mesoderm is also concerned with providing mechanical support for the animal is obvious, but in my opinion its contractile function is the primary one.

It cannot be stated with certainty at present that in the normal action of cœlenterate muscle this tissue is stimulated directly, though the investigations of Loeb on the jellyfish, Gonionemus, show beyond a doubt that such a method of stimulation is possible. It is, however, well established that in many jellyfishes muscle action is

under the influence, if not the control, of nerves, and these cases represent, so to speak, the second step in the differentiation of a neuro-muscular mechanism. In such jellyfishes, groups of cells especially open to stimulation by light, pressure, etc., occur on the edge of the bell, and from these sense bodies nerve fibers pass to the muscular sheet on the under face of the bell. These sense bodies evidently act as triggers by which the muscular mechanism can be brought into action and in that way render it more delicately responsive than if it relied entirely upon direct stimulation. The relation of such a system may be described as that of a set of sense organs directly connected with a musculature, for there is nothing here that can be fairly described as a central nervous organ. As the sense organs are in the ectoderm and the muscles represent incipient mesoderm, it is obvious that the future development of these two layers will in this respect be most intimately bound together.

The last organ, in my opinion, to appear in this chain of development is the central nervous organ, the brain and its subordinate centers. This originated on the line of connection between the sense organ and the muscle, but rather from the sensory than the muscular end, as is shown by its anatomical relations in adult animals and by its invariable origin in the embryo from the ectoderm. It is scarcely recognizable in the simple multicellular animals and begins to be an obvious organ in such intermediate forms as the worms. Here it serves chiefly as a means of freer and more extended communication between the sense organs on the one hand and the musculature on the other, and thus lays the foundation for the marvelous development that it shows in the higher animals, where, as a storehouse of race and individual experience, its significance is unparalleled. The paramount importance of the brain in fact is so fully recognized that it is usual to treat the sense organs as appendages of it, but, if the view that I have advanced is correct, just the reverse is true; the sense organs of a bilaterally symmetrical animal

are clustered at its anterior end not because the brain is there but because this is the end of the animal most likely to receive stimuli, and the brain is at this end because it has developed from this sensory equipment. The brain, in other words, is the appendage of the sense organs.

In tracing thus the growth of the three elements of the neuro-muscular mechanism, the muscle, sense organ, and brain, I have endeavored to keep before you their relations to those primitive organs, the ectodermic and entodermic cell layers, and to make clear to you how these cell layers come to be part and parcel of this growth. This subject might have been illustrated by any other set of organs than those concerned with the neuro-muscular mechanism; thus it is well known that the skeleton has been differentiated chiefly under the influence of the muscles, and that the digestive apparatus is as intimately associated with the differentiation of the circulatory organs as these are with the respiratory and excretory systems. But to discuss such relations even in a brief way would trespass too much on our present time, and I must therefore pass them by. Suffice it to say that in the main these relations constitute that province of zoology called by Goethe morphology, which includes the fundamental aspects of the form of adult and developing animals and which has been a field that for a century past has elicited the keenest interest from some of the most profound masters of zoology.

No one who has become deeply interested in morphological problems can have proceeded far without frequently meeting questions of a physiological nature. To answer these the simple observational methods of the past are insufficient, and it is necessary to resort to experimental procedure such as has been for a long time the practice of chemists and physicists. From this standpoint one enters what may be regarded as the most recent field of zoological research. Since the elementary substances of the animal body are the same as those of the inorganic world and since the stream of energy flowing

through that body conforms in large measure to principles already discovered in the physical and chemical laboratories, it has been generally assumed that the life processes of an animal are nothing more than complex examples of physico-chemical interaction. This idea has proved most stimulating in its effect on research, but to what extent it will be found true can not at present be stated. It is quite possible that the chemist and physicist have as much of a fundamental nature to learn from living material as they have already gained from lifeless substance.

The paramount influence of material in animal reactions can not better be illustrated than in such processes as inheritance. It is well known to you how much more closely on the average offspring resemble their parents than they do other members of their own species, and you are familiar with the long persistence of certain family traits. These resemblances are explained by the fact that the offspring start from a certain amount of living substance contributed by each parent, but the powerfully determinative qualities of this substance are only to be appreciated in certain cases. It is well known that in human beings there are two classes of twins, identical twins and ordinary twins. The latter come from two separate eggs and may vary as much from each other as any two members of the same family. The former come from a single egg which by some accident has become separated into two parts. Identical twins are always of the same sex and are often so alike in features and actions that they are almost indistinguishable even to their near associates. Their close similarity, which may amount almost to identity, shows that the substance from which they both came has developed in a most rigidly uniform way and indicates that the development of ordinary twins, as well as of other individuals, is probably also closely limited from the beginning, but the degree of this limitation is not discoverable in these cases, for we have no basis of comparison. Since living material can thus duplicate

itself in product, its significance in inheritance can not well be overestimated.

Not only may physical features be accurately inherited, but the capacity to perform various complex sets of actions may be transmitted with great precision. It is difficult if not impossible for us to state the exact source of many of our modes of actions. We inherit much and we learn much, and whether in a given complex act we are dealing with an inheritance or a new acquisition or a mixture is not always easy to state. With certain lower animals this question is perhaps more readily decided. Bees have the capacity of building a truly wonderful structure, the comb, which, because of economy of material and accuracy of workmanship, has long been an object of admiration. Is this complex activity inherited or learned by imitation? To answer this question, Kogevnikov reared some bees from a comb placed in an empty hive. After the bees had hatched and got their strength they proceeded without having seen other bees at work to make a comb that was as perfect as one made under ordinary circumstances. It might be objected that they had seen the comb from which they themselves had hatched, and this must be admitted to be so; but this fact is probably without significance, for they made perfectly typical queen cells the like of which they had never before seen. It is thus evident that not only structural peculiarities but highly complex activities can be inherited.

The means of this inheritance has already in a measure been made out. When a common protozoan, like Paramecium, reproduces, the parent body divides into approximate halves. Each of the two offspring receives not only a large portion of the parental substance but a certain number of cilia and other parts directly from the parent, and hence that the offspring should resemble the parent is not very surprising. When, however, reproduction in the higher multicellular animals is examined a somewhat different condition is discovered. Sexual reproduction is accomplished by means of a fertilized egg,

which consists of a mass of cytoplasm chiefly from the maternal side, a centrosome from the paternal side, and usually an equal number of chromosomes from each side. As the offspring may resemble both father and mother, it follows that the substance that is the vehicle of inheritance is very probably the material of the chromosomes, the chromatin. This chromatin carries from parent to child not the vestige of an organ and is inconceivably small in amount. The human egg cell is approximately a sphere with a diameter of about 0.2 of a millimeter, and with a specific gravity about that of water; consequently its weight is about 0.004 of a milligram. The volume of the chromatin of a fertilized mouse egg, as measured for me by Mr. J. A. Long, is somewhat less than one-thousandth of the volume of the whole egg, and, assuming that this proportion holds for the human egg, and that its chromatin has about the same specific gravity as water, the weight of this chromatin would be about 0.000,004 of a milligram. Yet this mere trace of material can influence the adult substance of two identical twins to such an extent that their bodily configuration and actions are scarcely distinguishable. If we estimate their combined weights to be 130 kilograms, the chromatin of the egg from which they came can be said to have influenced in this profound way 32,500,000,000,000 times its original weight. Of course it must be borne in mind that the chromatin of the egg is living and that in the growth of the individual it assimilates and thereby increases in volume; the chromatin is not spread through the growing body in ever-increasing dilution. But, even granting this, its precision in the transmission of characteristics is certainly most remarkable; for when it is derived from a single source, as in identical twins, its effect upon the growth of the two individuals is to make them most strikingly alike. It is important to observe that the chromatin of at least certain male cells is composed very largely of nucleic acids, and that it is therefore very probable that the chemical composition and structure of

these substances are intimately concerned with heredity. This discussion makes clear how extremely important certain materials are to the body and yet how impossible it is at this stage of scientific progress to frame any clear and consistent conception of the method by which these materials exert their influences.

If such relatively simple physiological questions as this concerning the material basis of heredity meet with difficulties such as I have pointed out, how vastly more intricate and perplexing must be the problem of the relation of the living materials of animals' bodies to their nervous and mental states. That such a relation exists is well recognized, but what this relation is will probably require many years even to outline.

It is in the direction of comparative physiology that the more important new advances in zoology are to be made. In my opinion zoology will meet with an expansion in this century quite as much as the study of electricity has in the last hundred years. When Franklin tried his hazardous experiment with lightning, no one suspected that he was dealing with a factor that could come to be of such paramount importance in every-day affairs as electricity has become, and it seems to me probable that the zoologist of to-day is working obscurely with problems that will eventually lead to revolutionary results. I have already pointed out the importance of certain minute quantities of material in inheritance, and the significance of this in animal breeding and in social problems must be evident. But in a thousand other ways the doings of animals are worthy of closest attention. Many of the most difficult problems that the human race has attacked have already found their solution among the lower animals. Secure aerial transportation, which is almost a dream with us, is an accomplished fact among many animals. Our own efforts are not so safe if they are more extensive than those of a flying fish. They are, however, by no means equal to those of a bat or an insect, and they are immensely inferior to those of a bird. Our

systems of artificial illumination are regarded by us as one of the many evidences of advanced civilization and yet our best products are ridiculously poor compared with those of the lower animals. Gas or other such luminants yield at best something less than one per cent. light, the remainder of the energy being dissipated as waste heat, and our most successful means of illumination scarcely reach fifty per cent. of efficiency. The radiant energy of the luminous organ of a fire-fly is all light, and none is wasted as heat. Were the processes of this organ understood and made applicable to daily life, they would at once sweep out of existence every illuminating plant known. Such a revolution as this suggests awaits only the advance of zoological science, and, as I have said, this may be looked for in the near future. To my mind it affords one of the brightest outlooks for zoological investigation.

Thus far I have scarcely touched on what has been for so long a time the rallying word in biological work, evolution. But, if we knew the physiological workings of the animal body, especially in relation to inheritance, etc., evolution would be in large part understood and the lines of work that have just been recalled would be only examples of evolutionary processes. The most promising recent change in the study of evolution, a change which we owe largely to de Vries, is the discovery that evolution as now understood is probably going on before our eyes and at a measurable rate; hence it is open to observational and experimental treatment and we may expect renewed and rapid growth in the near future for this line of work.

Many of the unexplored regions touched upon in this survey are of such magnitude that few can hope to be their conquerors, but all may aid in preparing the way. In invading these new regions former methods and means will be sure to be found insufficient; the help of kindred sciences, such as physics and chemistry, must be called upon. This appears to be a sufficient answer to those who thought that they saw in the subdivision of zoology and of other sciences a step away from the true unity of scientific endeavor.

NOTES AND LITERATURE

HEREDITY

The Possibility of Inheritance through the Placental Circulation instead of through the Germ Cells.—In the December issue of THE AMERICAN NATURALIST reference was made to Professor Bateson's explanation of the inheritance of hæmophilia. Hæmophilia is a tendency to excessive bleeding, ascribed either to "a peculiar frailty of the blood vessels or some peculiarity in the constitution of the blood." It is seen far more often in males than in females, yet the males do not transmit it. Physicians are so confident of this as to recommend that "the daughters should not marry as through them the tendency is propagated."

Professor Bateson compared the inheritance of hæmophilia with that of the horned condition in sheep. A hornless breed crossed with a horned form yields horned males and hornless females. The latter will transmit horns to their male offspring only, unless again crossed with horned stock, when horned females will also appear. This analogy with hæmophilia holds good in so far as the females transmit a condition which they do not present, and it suggests a possible explanation of the occasional manifestation of hæmophilia in females. It fails, however, in an essential point. The horned male sheep transmit their condition whereas the hæmophilic males do not.

A different explanation is suggested by the studies on immunity reviewed and supplemented by Dr. Theobald Smith.[1] Ehrlich, as he states, found that female mice which had been made immune to certain toxic substances gave birth to young which were also somewhat immune. The immunity was soon lost and was never transmitted to the second generation. Immune males did not transmit any immunity to their offspring. Other investigators, using rabbits and guinea-pigs, have shown the transmission of several forms of immunity through the females only.

The artificial immunity may perhaps be permanent in the parent guinea-pigs. It has lasted long enough to affect four litters of one female, and Smith has records of "a considerable

[1] Smith, T. The degree and duration of passive immunity to diphtheria toxin transmitted by immunized female guinea-pigs to their immediate offspring. *Jour. of Med. Research,* 1907, vol. 16, pp. 359–379.

number of guinea-pigs which transmitted immunity for over a year." One animal gave birth to a litter of immune young thirty months after receiving the immunizing injection. The immunity is not so well marked in the offspring, and Smith agrees with the general conclusion that the grandchildren of immunized females are never affected.

Ehrlich found that in mice lactation plays an important part in the transmission of immunity to offspring, and that normal offspring may gain a considerable degree of immunity by being nursed by immune mothers. This conclusion requires confirmation, for Vaillard and Remlinger agree that, in guinea-pigs and rabbits, nursing from an immune mother does not confer immunity.[2] Rosenau and Anderson[3] were able to exclude the milk as a factor in transmitting hypersusceptibility to serum injections by a series of "exchange experiments." In these experiments the offspring of a susceptible mother are given, immediately after birth, to a non-susceptible guinea-pig to nurse, and the young of the non-susceptible guinea-pig are placed with the susceptible mother. "From these exchange experiments we learn that the hypersusceptibility is not transmitted to the young in the milk."

Gay and Southard[4] believe that the well-known susceptibility of guinea-pigs to a second dose of horse serum is due to an unisolated substance which they name *anaphylactin*. This is probably transmitted from the blood of the mother to that of her young through the placental circulation. It is contained in the serum of a guinea-pig two hundred and four days after the animal has been made susceptible by the first injection, and if from 1.5 to 2.5 c.c. of serum from such an animal are transferred to a normal guinea-pig, the latter becomes susceptible. However, a transfer of serum from the second guinea-pig to a third does not produce susceptibility and this result corresponds with the observation that artificial immunity is inherited only by the first generation.

It is possible that hæmophilia is due to an abnormal chemical composition of the blood, such as produces its manifestations in the male rather than the female, owing to differences in metabo-

[2] Cited by Smith, *loc. cit.*

[3] Rosenau, J., and Anderson, J. F. Further studies upon hypersusceptibility and immunity. *Journ. of Med. Research*, 1907, vol. 16, pp. 381–418.

[4] Gay, F. P., and Southard, E. E. On serum anaphylaxis in the guinea-pig. *Journ. of Med. Research*, 1907, vol. 16, pp. 143–180.

lism in the two sexes. If its cause is a substance in the blood it may be "inherited" from the female alone, and the male which manifests the disease can not transmit it. Thus it would be a case of transmission through somatic elements rather than through the germ cells.

F. T. L.

INVERTEBRATE MORPHOLOGY

Form Variation in Amblystoma tigrinum.—Powers[1] has observed the aquatic forms of this salamander both in their natural environment and under artificial conditions. His paper contains a large amount of material of great interest which would be much clearer reading if the numerous observations and experiments had been more explicitly described as to objective point and methods employed. The paper is too long for condensation here, but a few of the results can be noticed and will be welcome to those interested in the axolotl question. He distinguishes two main types, the ordinary larvæ and the cannibals, both by habits and in important points of structure. Taking the ordinary form first, two types as a body form are recognizable: those with the habit of crawling about on the bottom in a sluggish manner and thus living largely in the dark, these are of a broader shorter form and are called the "robust type," and a second type of quite different habit, being active swimmers going about actively in search of their prey, and of an elongate slender form, the "slender type." There is a great difference in the ratio of head width to total length in these two types, head width being contained 6.42 in total length in the robust type and 11 times in the slender ones. The mode of feeding is quite different in these two types. In the robust bottom-living forms food is obtained by using the mouth as a sieve and opening it widely to strain water through it in hopes of finding food thereby, with the result that the gape is increased. On the other hand, the slender swimming forms go about actively in search of prey, which, when they see it, they actively seize so that the mouth is not opened so widely as in the sieving process of the sluggish robust type. He also notes variations in special parts, such as the tail, the head and the posterior limb. Tails vary

[1] Powers, J. H., '07. Morphological Variations and its causes in *Amblystoma tigrinum*. Studies from the Zoological Laboratory of the University of Nebraska, 71, pp. 1–77, pls. i–ix.

from broad to narrow, long to short, some are flat and some more rounded and tapering, thick and fleshy or thin. Heads vary in breadth, length, thickness, contour of muzzle, distance between nares, between eyes, size of gape of mouth. Hind limbs vary as to robustness or slenderness, rounded or flattened shape of toes and habitual position of limb with reference to body. The writer of the paper is inclined to refer most of the variations which he finds directly or indirectly to the nutrition of the possessor. He says "excessive nutrition with these larvæ seems as it were to overflow into all the peripheral parts quite regardless of function." He shows very satisfactorily that the foot features which seem like aquatic life adaptations are not such in fact, but are due to over-nutrition. In swimming these forms do not use the foot; it lies idly alongside the body.

The cannibal form of larvæ is very interesting and wholly novel. There are occasional larvæ which for reasons as yet unknown, and against the tendencies of most of the larvæ, have adopted the habit of feeding on their fellows. It was possible to convert some non-cannibal larvæ to the habit, while not even starvation would induce others to adopt it. Cannibals, a number of photographs of which are shown, are characterized by the great over-development of the head and under-development of the body and tail. The changes came on rapidly after the habit had become established, a week showing very marked steps in that direction. The head enlargement includes internal as well as external anatomical changes, gill arches become more elongated, more numerous and much larger teeth develop in the palatine region; the entire head becomes more elongated, the brain more posterior in position, and, more strange still, it "is easily seen through the soft palate . . . and is of a less compact and more piscine type." All these points need fuller and more detailed description and illustration than is given in the paper, and will doubtless receive further attention in a later work.

The paper is a valuable contribution to knowledge of the variations of Amblystoma; it does not add to the interesting problem of the cause of the non-transformation of the aquatic forms. We do not find ourselves in accord with the author's proposition to consider this a dimorphic species having a terrestrial and an aquatic form, for this seems to put the aquatic form on a par with the terrestrial one. The aquatic form seems too

occasional in occurrence and locality to justify this. We do not know but that all aquatic cases would have metamorphosed under suitable conditions, and the terrestrial form is indicated as being definitive by the anatomy of the circulatory and respiratory apparatus. Also we do not share Powers's objection to the name axolotl and siredon as a designation for the aquatic form; both have the sanction of general usage and do not apply to other animals, so that they are entirely clear.

H. L. O.

EXPERIMENTAL ZOOLOGY

Some Experiments on the Development and Regeneration of the Eye and the Nasal Organ in Frog Embryos.[1]—Dr. E. T. Bell has conducted a series of experiments on embryos of *Rana esculenta* and *R. fusca,* in which he found certain new facts in the development of the eye and nasal organ. Wolff had shown in 1894 that the crystalline lens of the salamander may be regenerated from the upper margin of the iris. Fischel also found later that the lens in the newt's eye would regenerate from the iris, and by wounding the iris in several places after removal of the original lens that one or more lenses were formed. Spemann, Lewis and others show in amphibian embryos that there is no localization of lens-forming material in any given area of the ectoderm, and that the formation of a crystalline lens depends directly upon the stimulation of the ectoderm, or outer embryonic wall, through contact with the optic-cup. Lewis in a series of interesting experiments in which he tranferred the optic-cup from its original connection with the brain to a more caudal position showed that when it came in contact with the ectoderm in this new region the optic-cup stimulated lens formation. In another instance the skin from the ventral surface of *Rana sylvatica* was placed over the optic-cup of *R. palustris* and gave origin to a lens.

Bell has discovered several other possible sources of origin for the crystalline lens. He cut off the optic-vesicle of the embryo and turned it completely around so that the former outer side now turned toward the brain; under these conditions the pigment layer of the retina itself was induced to form a lens-like structure. When the brain was opened in the mid-

[1] *Archiv für Entwicklungsmechanik der Organismen,* XXIII, pp. 457–478, pl. 14 to 20.

dorsal line and the right optic-vesicle of another embryo of about the same size was put completely inside, the brain tissue, provided it had not become too far differentiated, gave rise to a lens. In another case a lens was formed from the surface ectoderm although the cavity of the optic-cup was turned away from the surface. An optic-vesicle which came in contact with the early nasal organ caused this structure to form a lens. Finally, the lens of one eye budded off another lens to supply an optic-vesicle which was placed adjacent to it. Bell's experiments seem to show that all ectoderm cells before becoming specialized to any considerable extent have the power to differentiate into lens cells, though all of his experiments are not equally convincing.

A lens failed to form from the endoderm when the gut was opened and the optic-vesicle turned down into its cavity.

King with the frog and Dragendorf with the chick have shown that the optic-vesicle may regenerate when parts of its early structure are removed. If, however, the eye-forming region be completely destroyed these authors claim that no regeneration takes place. Bell, on the other hand, finds that when one lateral half of the brain is removed it will regenerate and at times an optic-vesicle forms on the regenerated side. He also removed, by means of fine scissors, the entire Anlage of the eye and found a new optic-vesicle to regenerate. The previous experimenters used heated needles for destroying the eye and Bell believes that this method injures the adjacent tissue from which regeneration might take place.

The formation of the pigment layer of the retina, Bell claims, is dependent upon the retina proper. There is also some evidence to show that the retina may cause undifferentiated epithelium to become pigmented when brought into relation with it at the proper time.

Bell finds that the optic, as well as the olfactory nerve, may be induced to follow a path that can in no sense be preformed.

The olfactory lobes of the brain when brought into contact with ectoderm out of the nasal region are unable to stimulate the formation of nasal structures. The nasal anlage is readily regenerated if removed at certain stages and its early development is independent of the parts of the brain and buccal epithelium with which it normally connects. The nasal structure is developed from a predetermined area of ectoderm and when this portion of ectoderm is transplanted to a position

above and behind the eye the nasal pit still forms and the olfactory fibers which develop in it grow into the lateral wall of the diencephalon above the eye, which is of course an unusual region for these nerve fibers to enter.

C. R. STOCKARD.

The Influence of Regeneration on Moulting in Crustacea.—A recent paper by Dr. Margarete Zuelzer[1] furnishes additional data regarding the influences of regeneration, or the replacement of lost parts, on the moulting process in crustacea. It is generally known that the members of this group have the power to grow new appendages, legs, antennæ or swimmerets, after the former ones have been lost through accident or injury. In order to produce the new limb as well as to grow, or increase in body size, the crustacean must moult its hard chitinous shell. The processes of growth are closely associated with moulting and the more frequently the animal moults the faster will it increase in size. When one of these animals has lost a limb it is usually replaced by a small new one during the next moult following the injury.

Since the moulting period is so closely connected with the normal rate of growth several investigators have endeavored to ascertain what effect regeneration might have on the interval between these periods. Zeleny found that crayfish while regenerating their limbs moult faster, or more frequently, than normal individuals, and, further, he holds that an animal regenerating several limbs moults more frequently and regenerates the limbs faster than one replacing a single appendage. He concludes that during regeneration the moulting process is hastened. Emmel, on the other hand, has reached an opposite conclusion from the study of a large series of young lobsters. He finds normal individuals moulting more frequently than others which are regenerating new limbs. Lobsters that have lost several appendages moult slower than those that have lost fewer. Emmel, therefore, believes that regeneration retards the moulting process. He showed very clearly that an important factor, which Zeleny had failed to take into account, was the time at which regeneration was introduced into the moulting cycle. If the limbs were removed the day after moulting the moulting period remained almost normal, but when the limbs were removed four days after the moult the resulting regeneration

[1] Uber den Einfluss der Regeneration auf die Wachstumsgeschwindigkeit von *Asellus aquaticus* L. *Arch für Entwick.-Mech.*, XXV, Dec., 1907.

lengthened the interval before the next moult by eighteen per-cent. The longer the time intervening between a moult and the removal of appendages the longer the following moult was postponed through the influence of the resulting regeneration, although the less likely was regeneration to ensue.

Emmel's experiments also seem to show that the retarding influence is due to the regeneration phenomenon and not to the injury sustained, since in all of his experiments those animals that failed to regenerate new limbs did not have the moult following the operation postponed.

In the young lobsters the regeneration process retarded their growth at times more than twenty-four per cent.

Dr. Zuelzer, having the contradictory results of Zeleny and Emmel in mind, has undertaken a similar study on the little crustacean Asellus. Agreeing with Zeleny, she finds that in the majority of cases moulting occurs at shorter intervals if regeneration is taking place. The rapidity of moulting depends upon the time elapsing between the last moult and the time of operation, an important factor, as shown also by Emmel.

If the animal is operated upon during the moulting stage or shortly after, the following moult is usually hastened by the regeneration phenomenon. When more time intervenes between the moult and the amputation of the limbs the tendency is to delay the first moult following the operation, but to hasten the second and third moults. Should the amputation of appendages immediately precede a moult the moult occurs normally, but no regeneration is shown, the next moult is retarded and regeneration occurs; the third moult is accelerated and the regenerating limbs increased in size. Occasionally when the operation preceded the moult by a considerable interval no regeneration occurred, although the moult may have been hastened.

When the two antennæ are cut at different levels so as to leave stumps of unequal lengths, the longer one regenerates at a slower rate than the shorter, so that the original equality in length is again established. Zuelzer considers this a case of "compensatory regulation," that is, the short stump influenced the longer one to regenerate slower than it would otherwise have done in order to reestablish their equality in length. This difference in growth rates may be equally well explained as due to the levels at which the cuts were made on the two antennæ, as Morgan has shown for the fish's appendage that the nearer

the edge or tip of a fin the cut is made the slower will be the rate of growth of the new tissue.

Repeated amputation, or removal of regenerating buds, continues to accelerate the moulting process. Zeleny has shown in Cassiopea, a jelly-fish, that repeated operation also hastens the rate of regeneration. New tissue grows faster from a cut surface that has previously regenerated tissue than from a newly cut surface that has not before regenerated.

Zuelzer finds, like Emmel, that the moulting time is unaffected, or she believes at times hastened, in those cases where regeneration fails to follow the amputation of appendages. The reason for this she thinks may be that the animal with fewer appendages has a smaller body mass and, therefore, more food to use in normal growth, particularly when none of this food is used to form regenerating tissue. Thus Emmel's lobsters which failed to regenerate moulted more rapidly than regenerating ones. When one considers, however, the apparent unimportance of food-supply on regeneration phenomena as shown by Morgan he becomes disinclined to accept Zuelzer's explanation.

In a general way Zuelzer agrees with Zeleny in that regeneration hastens the moulting process. It is interesting to note that both of these workers have used adult crustacea while Emmel's experiments were made upon larval or young lobsters and gave opposite results. A possible reconciliation of the results may be as follows: The young lobsters, like most young animals, are growing at a maximum rate; all available energy is being used in growth. When such animals are injured they receive a "set-back" since some of their energy must now be diverted in order to repair the injury. Emmel showed that the process of regeneration retarded the rate of growth of these lobsters sometimes more than twenty-four per cent., but when the injury was not repaired growth or moulting was not retarded. Adult animals, on the other hand, are not living up to their maximum possibilities; they are in an apparent state of reserve until the removal of an appendage or other injury excites them to new activities and regenerative growth begins. During regeneration the animal may be said to be in a condition of newly stimulated growth and all growth activities are probably influenced. One may predict that if similar regeneration experiments be tried on the adult lobster the results will agree with those obtained on adult crayfish and Asellus.

C. R. STOCKARD.

Experiments in Transplanting Limbs and their Bearing upon the Problem of Development of Nerves.—Students of nerve regeneration are divided into two camps according as they view the influence of the central or ganglion cell on the regeneration of peripheral nerve fibers. On the one hand it is assumed that no regeneration can take place in peripheral nerves that are isolated from their ganglion cell. On the other hand it is assumed that regeneration can take place in the complete absence of central influence. This is often spoken of as "autoregeneration."

The latter view finds its most recent exponent in Dr. Braus, of Heidelberg, who was led to it by the results obtained in transplantation experiments. He found that either the transplanted limb contained no nerves at all, or that functional nerves, typical in their distribution, were developed from any region of the body, whence they must have arisen *in situ* and secondarily come to unite with the ganglion cell.

A few details may be mentioned because of their extreme interest. Young tadpoles were used in which nerves had not penetrated to the limb buds. When such buds were transplanted to other regions of the body of a second tadpole, a limb developed in this bizarre position, quite normal in the structure of all of its parts, including its nerves. Posterior limb-buds were successfully grafted on the head, and posterior legs developed. As no nerves had been present in the buds at the time of transplantation, and as it seemed inconceivable to Braus that facial nerves, for example, could grow into the parasitic leg and show in the distribution of its parts an arrangement typical of normal limbs, he concluded that nerves must have developed *in situ*.

In a second series, the region which later gives rise to the nerve cells and fibers of the body was removed. Limb-buds from these "aneurogenic" individuals were grafted upon normal tadpoles and once again development of the limbs proceeded, but nerves were absent. If they grew centrifugally one should expect to find these limbs innervated by the outgrowing nerves from that particular region.

Professor R. G. Harrison, of Yale University, has rendered invaluable service in repeating and extending Braus's experiments, in a paper entitled "Experiments in Transplanting Limbs and their Bearing upon the Problem of Development of Nerves," in the *Journal of Experimental Zoology*, vol. 4, 1907.

In the first place, a careful examination of serial sections showed that nerves grow close to the region from which the transplanted buds were removed. The finer twigs of host and bud were thus brought into close union. It has been well established by a number of investigators that the union of the peripheral fiber of one nerve with the central fiber of another permits the functioning or regeneration of the former. This fact indeed is frequently taken advantage of in modern surgery. Similarly accurate examination of serial sections showed conclusively that, in the transplanted limbs taken from "aneurogenic" individuals, *nerves were present,* and that these were quite normal down to their minute details. There is thus presented the anomaly of a facial nerve, for example, growing along entirely new paths, whose direction is determined by the structures in the limb. Such distribution is thus not a function of the nerve, but of the organization of the limb which it innervates.

These more accurate methods revealed the further fact that accessory limbs, which are sometimes produced at the point of transplantation, also contain nerves often in a high degree of perfection. Braus had denied, on insufficient evidence, the presence of these nerves and had urged their absence as an argument opposed to their centrifugal growth.

By the aid of a very ingenious experiment, Harrison pushed the inquiry one step farther. "Aneurogenic" individuals, Braus and Harrison both found, were short lived. To overcome this difficulty, Harrison grafted an "aneurogenic" tadpole to the side of a normal or "nurse," and to the former he transplanted a limb-bud from a normal individual. A developing nerve was thus transplanted to a nerveless region. Though the results were not altogether satisfactory, the evidence pointed to the conclusion that "there is no progressive development of the nerve. On the contrary, there are rapid regressive changes, which in the majority of cases result in the entire disappearance of the nerves within a few days after they are cut off from their centers."

On the whole, though the paper is exceedingly accurate—a characteristic of Harrison's work—so far as it goes, it does not settle the question, especially in the light of Bethe's recent contribution. Perhaps, after all there is an element of truth on both sides, and just how much value to put to each is the problem to be decided.

A. J. G.

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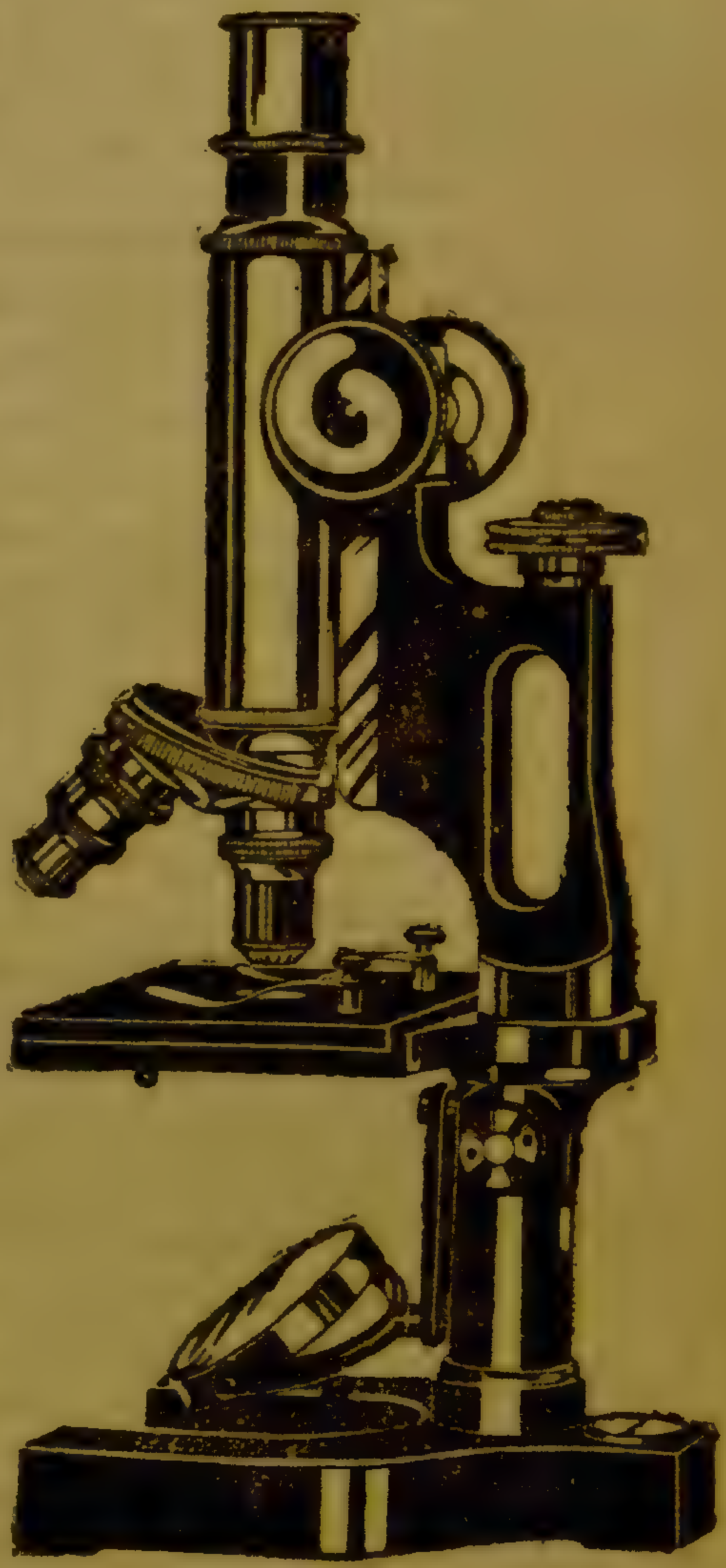

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PROFESSOR BASHFORD DEAN

Columbia University

Lamarck manuscripts are exceedingly rare. For until the last score years Lamarck was ranked as a discredited author, and his writings were thrown aside. Even the autograph collector, to whose nets almost everything is a fish, has hardly taken the pains to preserve his bare signature. The Harvard manuscript, accordingly, is an important document, especially in these days of Lamarckian revival. It is holographic, antedating, therefore, 1818–20, the years when Lamarck's eyesight was lost. It forms together a series of essays and drafts of later work, all in all about ninety leaves, of which fifty have writing on both sides. They are brought together in a volume with marbled sides and morocco back with the legend, "Manuscrits de Lamarck," the binding dating 1830–40. As a frontispiece there is inserted the Langlumé lithograph of Alexis Noël's portrait of Lamarck (1823). Following this is a table of contents, probably in the hand of the early owner of the manuscript. It reads:

Manuscrits | de | J. B. P. A. de Lamarck | Membre de l'institut de france, Professeur-admi- | nistrateur du Museum d'histoire naturelle, ect. contenant|.

1° Système de Gall.......................... 20 fuillets
2° Idée et Imagination .... 19 "
3° Apperçu analytique de connaissances humaines. 11 "

4° Questions Zoologiques........................	9	"
5° Histoire naturelle	3	
6° Planches préparées pour les figures des genres qui feront partie de la 2ᵉ édition des animaux sans vertèbres............................	19 fuillets	
Total	81 fuillets	

From this it will be noted that the papers were collected before 1835, the year of the appearance of the second edi-

Jean Baptiste, Pierre-Antoine Monet de Lamarck.

tion of the "Animaux sans Vertèbres," for it is stated that the drawings *will form* part of the second edition, not that they did form part of it.

This manuscript was presented to Harvard University in 1896 by Professor Alexander Agassiz, who appears to have discovered it in Paris. Its earlier provenance is unknown. My attention was called to it by my friend,

questions zoologiques
dont la solution est de première importance.

1ère question : les animaux et les végétaux étant des corps vivans, ces 2 sortes de corps se confondent-ils par un point commun des séries qu'elles forment ; ou existe-t-il quelque caractère exclusif et tranché qui distingue nettement les premiers des seconds ?

2e question : peut-on mettre en évidence, par la citation de faits décisifs, que tous les animaux connus jouissent du *sentiment* ; ou qu'il n'y a qu'une partie d'entr'eux qui soient doués de cette faculté ?

3e question : peut-on prouver par des faits pareillement décisifs, que tous les animaux connus possèdent la faculté d'avoir des *idées* et de former cette détermination par préméditation qui fait agir *volontairement*, et permet de varier les actions ; ou qu'il n'y a qu'une partie des animaux qui jouissent de cette faculté ?

4e question : y a-t-il quelque faculté animale qui ne soit pas un phénomène d'organisation et qui soit indépendante de tout système d'organes quelconque ; ou toute faculté qui n'est pas commune à tous les animaux, ne dépend-elle pas d'un système particulier d'organes qui y donne lieu ?

5e question : tous les animaux connus possèdent-ils la totalité des systêmes particuliers d'organes qui composent l'organisation très compliquée des animaux les plus parfaits ; ou, quoique ces systêmes d'organes soient essentiels à la vie dans les ~~organi~~ animaux qui les possèdent, la vie dans d'autres animaux ne peut-elle pas exister

A Page of the Harvard Manuscript (p. 113).

Dr. C. R. Eastman, who was generously instrumental in placing it in my hands. To him, therefore, and to Professor Samuel Henshaw, curator of the Museum of Comparative Zoology, my thanks are due for the privilege of examining it.

In further detail, and in the matter of its published or unpublished parts:

The *Système de Gall* is largely medical: it deals with the brain, its anatomy, comparative anatomy, physiology, pathology—the last in some detail as in idiocy, cretanism, suicidal mania, hereditary insanity. I cannot find that it has been published.

The second essay, *Idée et Imagination,* has certainly been published. It bears the note in Lamarck's hand, "*Articles du diction,*" and is signed by compositors. Dr. Eastman suggests that it occurs in *Nouv. Dict. Hist. Nat.* of Detérville, 1818, a work I have not been able to consult. The writing indicates an earlier date than the remaining leaves.

The third portion, *Apperçu analytique des connaissances humaines, avec des divisions et des reflexions tendant à montrer leur degré de Certitude, leurs Sources, leurs Branches principales,* is probably the outline of his extended work (362 pp.) on the same subject published in 1820: it is entirely in his own hand and probably dates not later than 1818 (the year in which his eyes failed him).

Of the fourth manuscript, *Questions Zoologiques,* the first section is substantially as follows:

"Zoological questions whose solution is of first importance.

"*First Question.*—Animals and plants being living bodies (corps), do these two kinds of organisms become confused (se confondent) at a common point of the series which they form; or does there exist some exclusive and trenchant character, which distinguishes sharply the first from the second?

"*Second Question.*—Can one show by the citation of decisive facts, that all animals known are endowed with sensation;[1] or that there are only certain of them which are endowed with this faculty?

[1] Lamarck uses the word "sentiment." From several contexts, however, one concludes that more than "sensation" is intended, and that "con-

"*Third Question.*—Can one prove by facts equally decisive that all animals known possess the faculty of having ideas and of determining them by premeditation,—a premeditation which is formed *voluntarily* and which permits the actions to be varied; or are there only certain animals which enjoy this faculty?

"*Fourth Question.*—Is there some faculty in animals which is not a phenomenon of organization and which is independent of all systems of organs whatever; or does not every faculty which is not common to all animals depend for its origin upon a particular system of organs.

"*Fifth Question.*—Do all animals known possess the totality of the particular systems of organs which make up the very complicated organization of the most perfect animals; or, however essential are these systems of organs to the life in the animals which possess them, can not life in other animals exist without them?

"*Sixth Question.*—Is there known a single organ which is essential to animal life (in general) whatever be its function in the particular organism of which it forms a part; or must we not assume that life, whether of plant or of animal, needs no particular organ whatever, to enable it to exist in certain organisms.

"*Seventh Question.*—Cannot *sensation* (*sentiment*) and *irritability* be regarded as one and the same organic phenomenon and can it not be proved by facts that every portion of an animal which is endowed with *irritability* is also endowed with *sensation;* or is not *irritability* with which all animals are endowed, whether in all their parts or in certain of them only, an independent phenomenon and distinct from the *sensation* enjoyed by many animals?

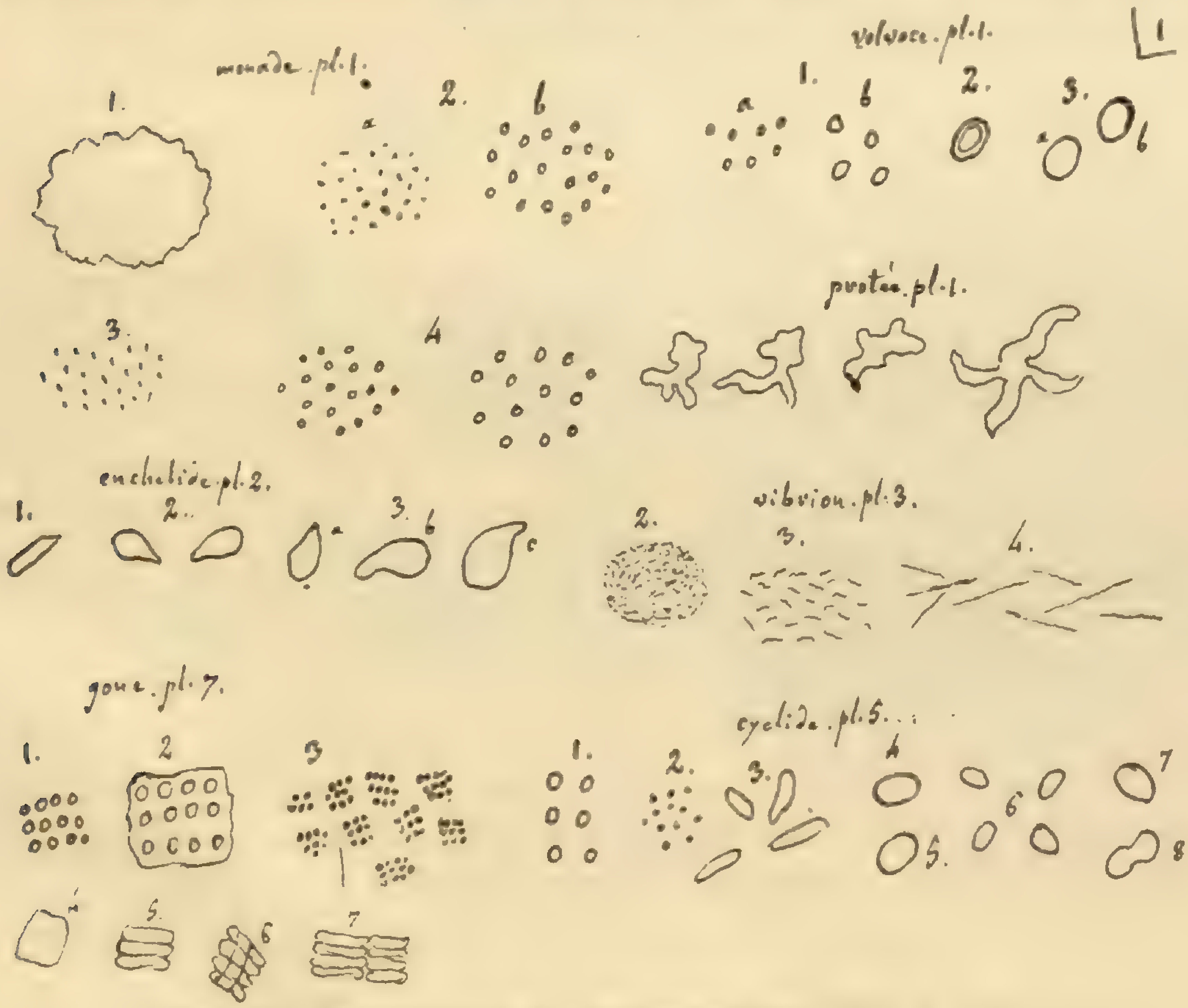
"*Eighth Question.*—Can it be established clearly that the facts of movement in the case of so-called *sensitive* plants demonstrate in these plants either *sensation* or *irritability;* or that these facts have no relationship whatever with those which demonstrate in animals on the one hand *sensation* and on the other *irritability?*

"*Ninth Question.*—The nerves alone are the organs of *sensation* since

sciousness'' might often be the better rendering. Thus in the eighth question referring to sensitive plants he distinguishes sharply ''sentiment'' from ''irritabilité.'' The latter gives the idea of unconscious reflex to stimulus, and the former then becomes antithetic, *i. e.*, conscious. The literal text in this question reads ''peut on établir d'une manière evidente, que les faits de mouvement relative aux plantes dittes *sensitives*, constatent dans ces plantes soit le *sentiment*, soit *l'irritabilité;* ou que ces faits n'ont aucun rapport avec ceux qui attestent les uns le *sentiment*, les autres *l'irritabilité* des animaux?'' Again, contrasting questions second and third, it is clear that ''sentiment'' in the second question is distinguished from a higher form of consciousness, which is equivalent to reason (or intelligence). In general we assume that the phrase ''avoir le sentiment'' implies consciousness.

the faculty of sensation is lost in a part (of an animal) in which the nerves supplying it have been destroyed; now the question is whether every nerve produces a sensation when it is affected, and whether the nerves which bring the muscles in action as well as those which furnish the forces of action to the organs produce sensation, like the rest; or whether there are not particular and special nerves for the production of sensation, while the others function some for *muscular excitation,* the others only for putting different organs in a condition to execute their functions?

"*Tenth Question.*—Is there some constant and peculiar sign which will make us understand that a being differing from ourselves ex-



Lamarck's Pen-drawings of Microorganisms (MS. p. 145).

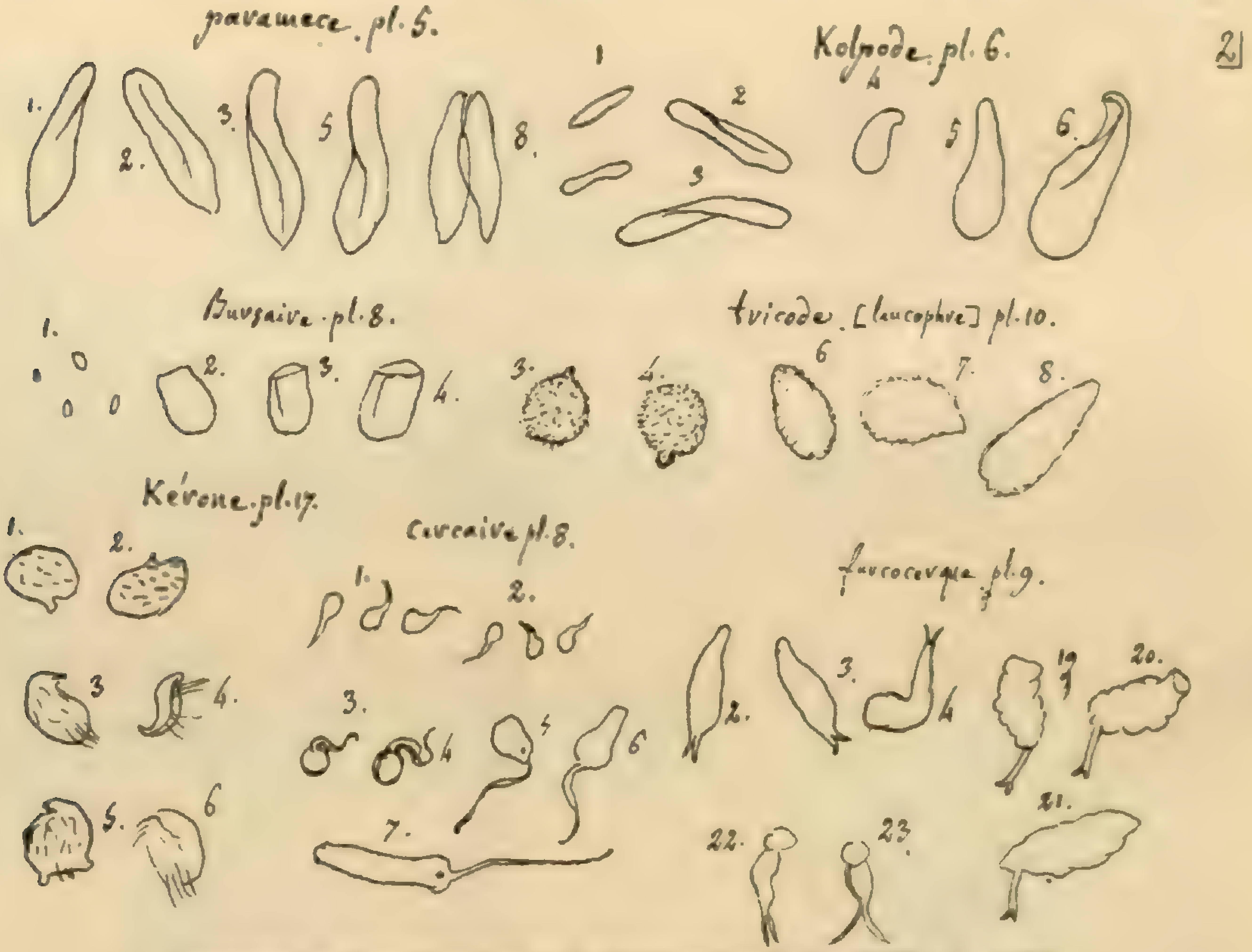
periences a sensation when it is stimulated (*affecté*), and can one always accept as a test the similar movement which it then executes; or, however in general an animal gives no other sign of a sensation produced than by the movements of its parts, can not these movements often deceive us and be due only to the *irritability* excited in the parts of the animal?

(I know no certain sign of a sensation produced save a *cry* evoked by pain: but all animals are not able to give such a sign and those which have the power do not always use it.)

"Supplemental Question:

"*Eleventh Question.*—If each particular system of organs gives rise to a particular faculty, can this faculty be found again in an animal in which the system of organs which produces it no longer exists; or can not this same faculty be regarded as destroyed when the system of organs which has given rise to it ceased to exist?"

These questions date from the period 1810–18, with the probability that they belong nearer the later than the earlier date, for in his "Philosophie Zoologique" (1809)



Lamarck's Pen-drawings of Microorganisms (MS. p. 147).

his views were by no means as advanced. He then spoke of the essential differences which distinguish plants and animals, and did not query their common origin, and did not seek a trenchant character which would serve to distinguish them. Moreover, he did not then query the possible kinship of sensation and irritability in sensitive plants and in animals, for at that time he had seen no reason to deny the elastic-fluid explanation for the sensitive movements of plants. Altogether these questions are of considerable interest in the study of the develop-

ment of Lamarck's views. They had, however, hardly reached the level of his Introduction to the second edition of his "Animaux sans Vertèbres" (1835). But we can regard them as sure steps in that direction, for similar ideas are here and there found in the Introduction. Indeed the second part of these Questions Zoologiques, MS. pp. 117–130, undoubtedly served as a first draft of this. Thus the present p. 117 is equivalent to p. 17 of the Introduction, and one can identify nearly all of the remaining leaves.

The fifth portion is headed "Histoire naturelle," and deals with its scope. It appears to have been a draft of a portion of the second edition of the "Animaux sans Vertèbres," for it is captioned *"Chap. 4. Connaissance des Corps organisés vivans que s'observent à la surface de notre globe et dans les eaux liquides,"* but these lines have been crossed out. The same ideas occur in the published work but in different form, so it is perhaps unnecessary to append here the entire section. The last page will give an idea of its tenor:

A Color-drawing of a Holothurian.

"Living bodies and inorganic bodies are the materials of natural history. They compose together the mass of the terrestrial globe, but they occur in very different proportions, for the first form a portion exceedingly small, while the second constitute almost the totality.

"Yet the bodies which are possessed of life are innumerable in the diversity of their species, and those, on the other hand, which lack it, exhibit in proportion only a small number. Indeed, we know hardly more than six or seven hundred species of minerals, while the number of species of living bodies can not be estimated as less than 100,000.[2]

"These considerations are not lacking in interest, provoking our reflections, and each one of them presents us a fact, an item of knowledge with which we have to reckon. In a word these singular bodies which possess life, which are so diversified, are yet the constituents of but a very small portion of the globe which man inhabits."

The final pages of the manuscript contain the following drawings:

Plate I, monads, volvoce, enchelide, protée, vibrion, goue, cyclida.

Plate II, paramèce, kolpode, Bursaire, tricode [leucophre], Kérone, cercaire, furcocerque.

Plate III, Ratule, tricocerque, vaginicole, folliculina, Brachion, furculaire.

Plate IV, urcéolaire, vorticelle, tubiculaire.

The remaining pages include the "animal of lepas balanus," with parts named, "millipora gelatinosa," a color sketch, a number of jelly fishes, including "dianée triedre," "orythie verte," "orthie hexaneme," "dianée proboscidale," "dianée dineme"; a number of nudibranchs, pteropods, and a beautifully colored drawing of a living holothurian.

[2] A generous estimate for that period—a number now several times exceeded within the insecta.

SYMBIOSIS IN FERN PROTHALLIA

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THE symbiotic associations so frequently met with in plants present one of the most interesting phenomena with which the biologist has to deal. While these associations are often not easily distinguishable from true parasitism, in many instances there is a genuine symbiotic relation and, although there may be a certain degree of parasitism, there is no question that these associations are for the most part beneficial to both of the forms concerned. Indeed, the very existence of one or both of the symbionts may depend upon it.

In most cases of symbiosis, one of the symbionts is a fungus, but this is not always so. Certain of the Schizophyceæ or blue green algæ are very commonly associated with higher plants in what appears to be a symbiotic relation, although the nature of the association in this case is still very obscure. The Anthocerotaceæ and several of the liverworts, like Blasia, always have within their tissues colonies of a Nostoc, and the little water fern Azolla invariably harbors in each leaf a colony of the Nostoc-like *Anabæna Azollæ.* Nostoc has been found to occur in the roots of *Cycas revoluta* and Gunnera among the seed plants, and the Schizophyceæ also frequently constitute the "gonidia" of many lichens. The association of the nitrogen-fixing bacteria with the root nodules of the Leguminosæ is also a well-known case of symbiosis. Of the true algæ there are a number of species recorded, *e. g., Chlorochytrium Lemnæ,* which live within the tissues of higher plants, but it is doubtful whether the host is in any way affected by the presence of the alga, which

presumably secures lodging, but not board, from its host.

The symbiotic association of fungi with green plants was first demonstrated in the lichens, but it is now known that many of the higher plants are regularly associated with fungi in what is undoubtedly a symbiotic relation. The best known cases of these are the mycorhizal fungi connected with the roots of many trees, especially the Cupuliferæ, and those which occur in the tissues of saprophytes growing in humus. These humus saprophytes are especially numerous among the Orchidaceæ, *e. g.*, Neottia, Corallorhiza, Cephalanthera, etc., and in certain forms of the Ericales. The well-known Indian pipe, *Monotropa uniflora,* and the snow plant of the Sierra Nevada, *Sarcodes sanguinea,* are well known examples of these saprophytic Ericales. Many Orchidaceæ and Ericaceæ which possess chlorophyll are also to a greater or less extent saprophytic and show a well-developed mycorhiza. In the case of chlorophylless plants, there can be little doubt that the fungus enables them in some way to utilize carbonaceous compounds from humus. In the case of plants such as the trees referred to, where there is ample chlorophyll tissue, it is more likely that the rôle of the mycorhiza is rather to supply nitrogen than carbon, and it is highly probable that in the case of chlorophylless saprophytes as well, the fungus provides nitrogen. This has recently been demonstrated for the mycorhiza found in the roots of various Ericaceæ, *e. g.,* species of Erica, Vaccinium, Calluna and Oxycoccus[1] In all of these it was shown that the fungus concerned, which seemed to be a species of Phoma, was able to assimilate free nitrogen in much the same way as is done by such nitrogen bacteria as Azotobacter.

A very complete study of the endophytic fungi of roots has been made by Janse.[2] He examined a very large

[1] Dr. Charlotte Ternetz. Über die Assimilation des atmosphärischen Stickstoffes durch Pilze. *Pringsheim's Jahrbücher,* XLIV, July, 1907.

[2] Les Endophytes Radicaux de quelques Plantes Javanaises. *Ann. du Jardin Botanique de Buitenzorg,* XIV, 54–201, 1895.

number of plants, mostly phanerogams, but also a number of liverworts and pteridophytes. His researches showed the presence of an endophytic mycorhiza in a surprisingly large number of plants belonging to the most diverse families, from Zoopsis, one of the Hepaticæ, to Vernonia, a genus of Compositæ.

The study of the mycorhizal fungi of the seed plants has called attention to the presence of similar fungi in the pteridophytes. The occurrence of a mycorhiza in the roots of the Ophioglossaceæ was first shown by Russow.[3] In 1884 Treub described a similar fungus from the gametophyte of Lycopodium. In his very important paper on the prothallia of Lycopodium[4] he pointed out the universal occurrence of this fungus in *L. cernuum,* and in later papers he showed that this also occurred in *L. phlegmaria,* as well as in some other species, but it was apparently absent from the green prothallium of *L. salakense.* In 1895 I called attention to the presence of a similar endophytic fungus in the subterranean prothallium of *Botrychium virginianum.*

The past decade has been notable for the numerous important investigations upon the gametophytes of the Ophioglossaceæ and the Lycopodiaceæ and our knowledge of these is now quite complete, thanks to the labors of Bruchmann, Lang and Jeffrey. It is clear that in all prothallia of the subterranean, and hence purely saprophytic type, an endophytic fungus is invariably present. It has also been shown that a similar form occurs in the green prothallium of some species, at least, of Lycopodium; but so far as I am aware its occurrence in the green prothallium of ferns has not hitherto been recorded.

Some time ago, having occasion to look over slides of the prothallium and embryo of *Osmunda cinnamomea,* it was noted that many of the prothallia contained an endophytic fungus very similar to that found in Botrychium

[3] Vergleichende Untersuchungen der Leitbündelkryptogamen. *Mem. de l'Akad. Imp. des Sc. de Petersbourg,* 1872, XIX, 107–118.

[4] Etudes sur les Lycopodiacées. *Ann. du Jardin Botanique de Buitenzorg,* IV, 1884.

and Ophioglossum. This suggested the possibility of its occurrence in other green prothallia, and the forms which seemed to promise best were the Marattiaceæ, which in many ways seem to be the nearest relatives of the Ophioglossaceæ, in whose subterranean prothallia the endophyte regularly occurs. I therefore made an effort to obtain prothallia of the Marattiaceæ while collecting in Ceylon and Java, and procured prothallia of *Angiopteris erecta* Hoffm, *Kaulfussia æsculifolia* Bl., and *Marattia sambucina* Bl. The two former were carefully studied, and as was expected, the endophyte was found in nearly every case. The prothallia of *Marattia sambucina* were not examined, but the examination of a series of sections of *M. Douglasii* Baker, made some years ago, showed that in this species the endophyte was also present and presumably it occurs also in other species of Marattia.

The other family of ferns in which it was thought the endophyte might occur was the Gleicheniaceæ, a small family, mostly tropical and of wide distribution. The Gleicheniaceæ are considered to be related to the Osmundaceæ and it was thought that they also might show the presence of the endophyte. The prothallia have rarely been collected, but are not difficult to find if one looks for them carefully. Material of four species was secured, one being collected near Cape Town, the others in Ceylon and Java. In all cases the endophytic fungus was found in the older prothallia.

These investigations show conclusively that an endophytic fungus is normally present in the green prothallia of several Marattiaceæ, Osmundaceæ and Gleicheniaceæ, and it is highly probable that further research will show similar fungal endophytes occurring in the prothallia of many other ferns.

The Structure of the Endophyte

Since the discovery of the endophytic fungus in the gametophyte of Botrychium, it has been found constantly

in all the investigated species of Ophioglossaceæ, and it is safe to assume that it is invariably present and is essential to the growth of the gametophyte.

The writer has recently had occasion to study the behavior of this endophyte in the gametophyte of several species of Ophioglossum and has described and figured this somewhat at length.[5] The fungus consists of non-septate, large, branched hyphæ, which are strictly intracellular, passing from cell to cell through the cell walls, and they may often be traced for long distances. In all of the forms that have been investigated the fungus is confined to the older parts of the gametophyte, and never invades the meristematic tissues nor the tissues in the neighborhood of the young reproductive organs. There is in the cylindrical branches of the gametophyte of Ophioglossum a more or less definite infected zone inside the superficial tissues, while the central region remains almost entirely free from the endophyte. Sometimes fragments of mycelium are found upon the outside of the gametophyte, and these may occasionally be found to penetrate into the rhizoids and thus gain entrance to the inner tissues. The infection, however, probably in all cases takes place first while the gametophyte is still composed of very few cells. This was positively demonstrated in the germinating spores of *O. pendulum,* where only those young prothallia which succeeded in establishing a connection with the fungus developed beyond a three or four-celled stage. Otherwise they died after the nutrient matter in the spore was exhausted. Secondary infections, however, doubtless take place frequently. The form of the fungus growing outside of the prothallium is quite different from that within its tissues. The hyphæ in the former case are more slender and sometimes septa may be formed, while these seem to be quite absent from the endophytic hyphæ.

In material fixed with chromic acid, the structure of

[5] Campbell. Studies on the Ophioglossaceæ. *Ann. du Jardin Botanique de Buitenzorg,* XXVI, 1907.

the hyphæ is well shown. The walls, which in the ordinary hyphæ are moderately thick, stain well with gentian violet, while in the finer granular cytoplasm there are more or less numerous small bodies which stain strongly with safranin and are with little question nuclei. Some of the cells of the host contain unmodified hyphæ, which may be so numerous as to fill the cell cavity with a dense coil of filaments. In other cells the hyphæ form masses of irregular swollen vesicles with much more delicate walls than the ordinary hyphæ, and sometimes quite filling the cell. Besides the irregular vesicular swellings of the hyphæ described above, there may occur large oval or round structures (Fig. 1) which resemble the young oogonia of Pythium or Albugo. These may have a diameter of nearly 50 μ, but are usually smaller. The nuclei in these bodies are more numerous than in the vegetative hyphæ, and finally may be very conspicuous (Fig. 1, *C*). This multiplication of the nuclei resembles the preliminaries of zoospore formation in the sporangia of Saprolegnia or Pythium, and occasionally there were seen free in the host cells small bodies that looked as if they might have been discharged from these large oogonium-like bodies. The latter are probably identical[6] with

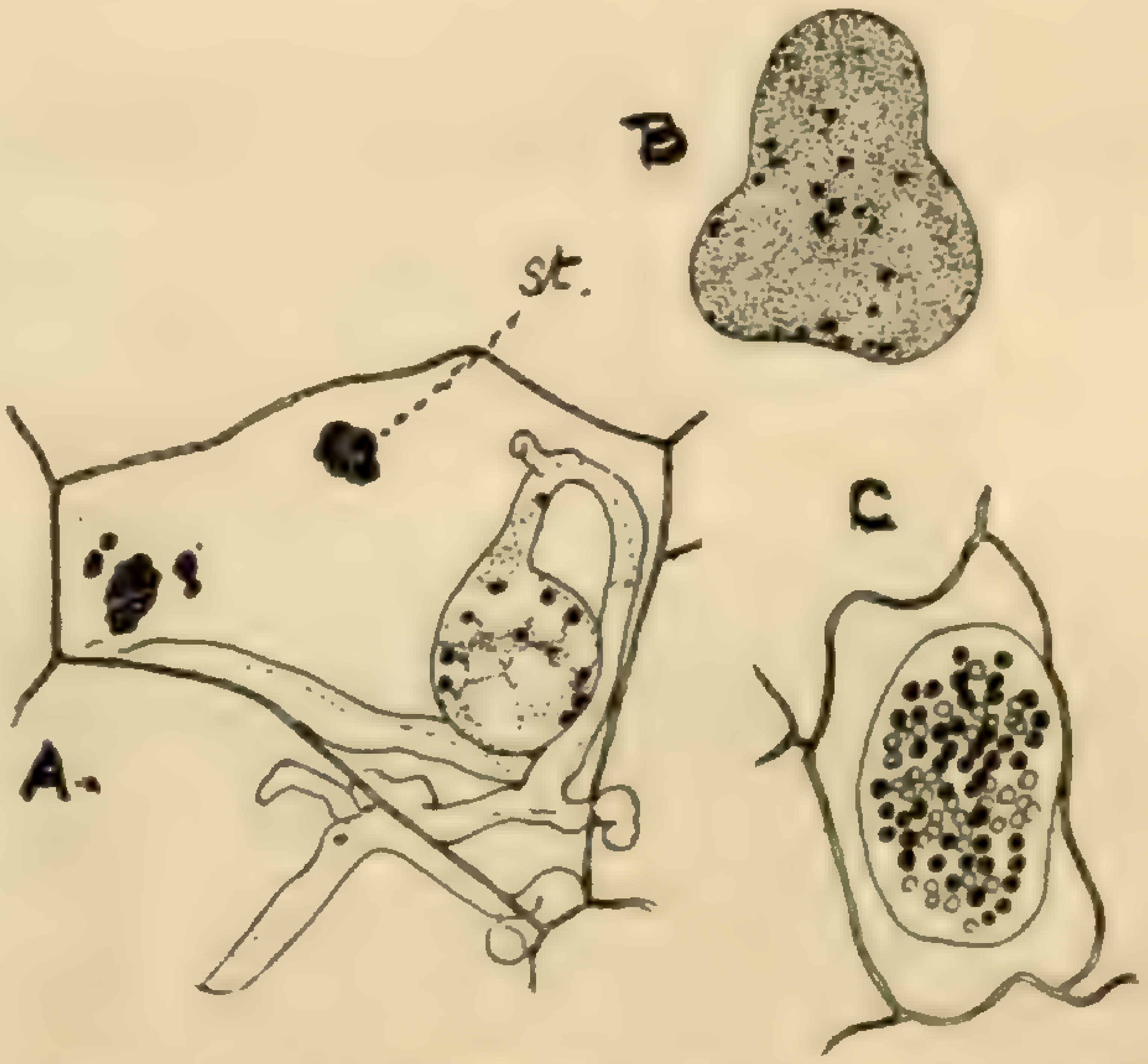

FIG. 1. *A*, Cell from the gametophyte of *Ophioglossum pendulum*, showing the mycelium of the endophyte, and a young conidium (?); *st*, masses of disintegrating starch granules; *B*, large conidium (?) of the same; *C*, fully developed conidium (?), showing the numerous enlarged nuclei; all × 350.

[6] Jeffrey. The Gametophyte of *Botrychium Virginianum*. *Proc. Canad. Institute*, V, 1898.

the "conidia" described by Jeffrey in Botrychium, but do not show the thick walls of these conidia. Like these conidia of Botrychium they are not, usually at least, separated from the filament by a septum. The young cells of the gametophyte contain starch in the form of rather small and very distinct granules. As the endophyte invades these cells, the starch granules soon show evidences of disintegration, swelling up and losing their sharp contour and finally becoming aggregated in irregular masses of considerable size (Fig. 1, *A, st*). These finally are more or less completely digested by the fungus, but the nucleus of the host cell is in no way affected, and even where the cell is completely filled with the crowded hyphæ, the nucleus remains quite normal in appearance.

The endophyte of *Botrychium virginianum* (Fig. 2) closely resembles that of Ophioglossum, but is somewhat smaller in all its parts and occupies the whole central region of the massive gametophyte. The two sorts of

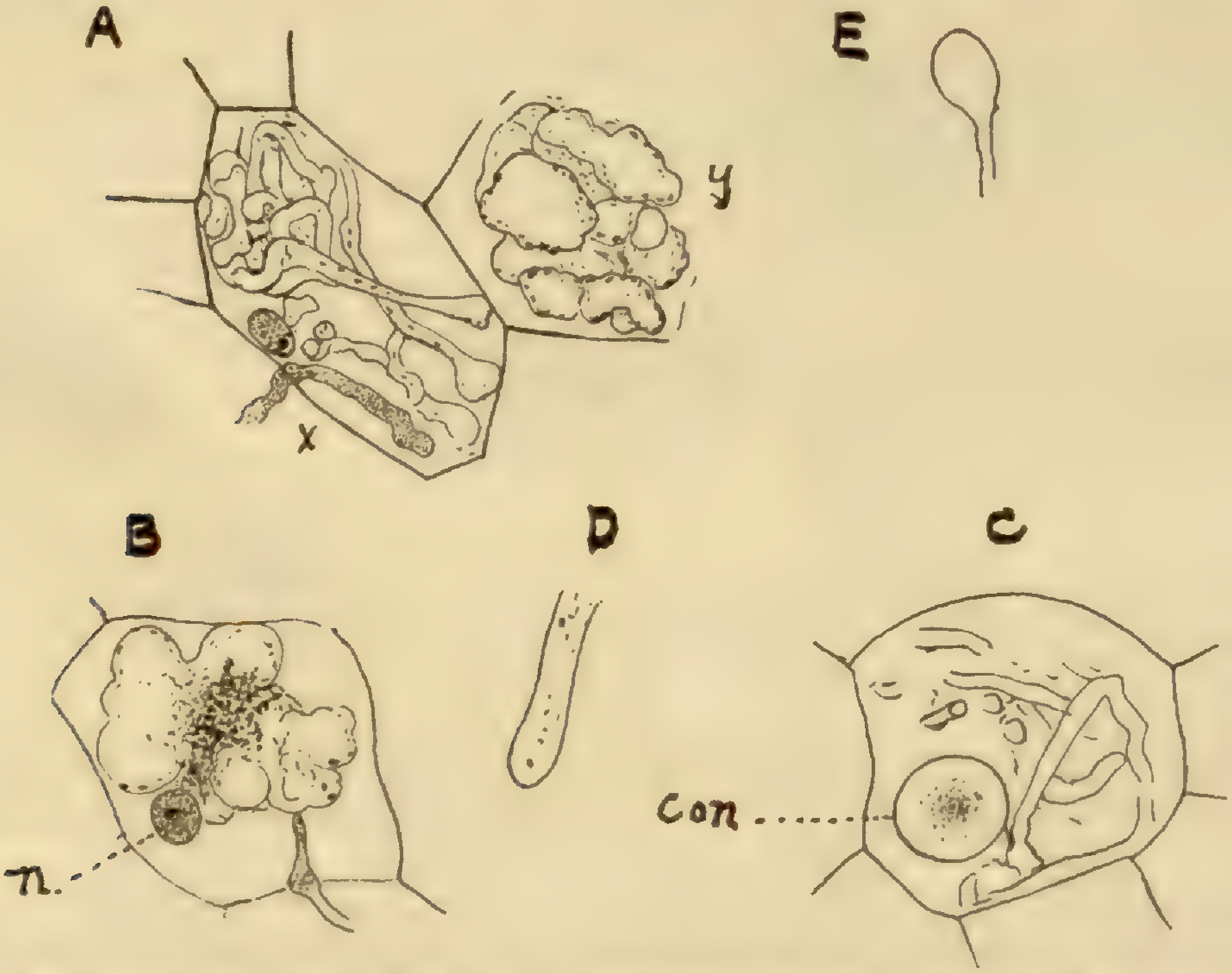

FIG. 2. *A*, two cells from the gametophyte of *Botrychium virginianum*, showing the two forms of the endophyte; *B*, a "digestive" cell, showing the degenerating varicose mycelium of the endophyte; *n*, the nucleus of the host cell; *C*, cell containing a conidium, con; *D*, fragment of one of the largest hyphæ; *E*, young conidium. All figures × 350.

cells, *i. e.*, those with the filamentous hyphæ (Fig. 2, *A*, *x*) and those containing the irregular vesicular mycelium, (*y*), are well differentiated, but are more or less irregularly mingled. The "conidia" (Fig. 2, *C*, *con*) are smaller and less numerous than in the endophyte of Ophioglossum, but have a much firmer membrane, as Jeffrey has described. These conidia were observed by Jeffrey to germinate by sending out a tube, and they are supposed to be special organs of propagation.

In a very important study of the endophytic mycorhiza of the saprophytic orchid, Neottia, W. Magnus[7] has shown that two types of mycelium exhibited by the endophytes are of very different nature. The slender cylindrical hyphæ constitute the active portion of the fungus, which behaves like a parasite toward the cell which it invades, destroying the starch and probably other constituents of the cell, but not attacking the nucleus. The latter becomes much hypertrophied, a phenomenon that is not seen in the endophyte of the Ophioglossaceæ. The swollen vesicular mycelium, however, is a degenerating structure and is itself destroyed by the cells of the host, which actually digest these fungus mycelia in much the same way that the cells of Drosera digest their prey. Some interesting similarities in the behavior of the contents of the digestive cells of Drosera and those of these humus saprophytes have been demonstrated. Figs. 2, *A* and *B*, show some of these cells in Botrychium; the varicose mycelium has very delicate walls, and in the older cells (Fig. 2, *B*) they seem to be disintegrating until finally the structure is completely destroyed and only a structureless lump is left. In Neottia this undigested mass is ejected into a central vacuole and becomes surrounded with a more or less evident cellulose membrane, separating it entirely from the protoplast after digestion is complete.

A comparison of the endophytes found in the green

[7] Studien an der Endotrophen Mycorhiza von Neottia Nidus Avis L. *Pringsh. Jahrb.*, XXXV, 1900.

prothallia of the various ferns referred to shows some differences which are probably not without significance. The structure of the mycelium and its general behavior are so much like those of the endophyte occurring in the strictly saprophytic gametophyte of the Ophioglossaceæ as to leave little doubt that the endophyte in each case

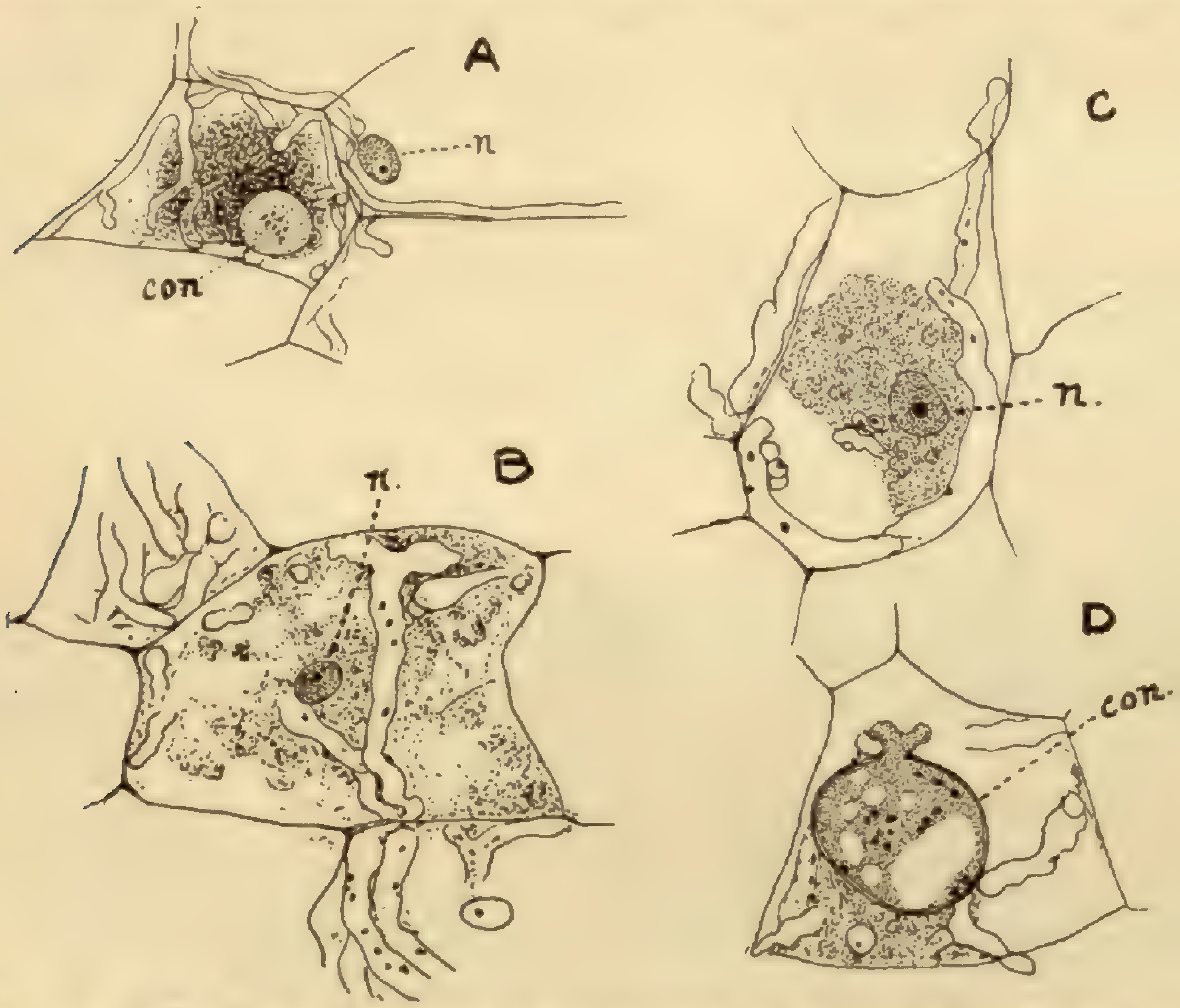

FIG. 3. Cells from the green gametophytes of several ferns, showing the character of the endophyte. All figures × 350.
A, Angiopteris evecta; B, Osmunda cinnamomea; C, D, Gleichenia pectinata.

is the same, or at any rate closely related. The conidia (Fig. 3, *A, C*) are perhaps less frequent, but in form and structure are very like those of Botrychium. The most noticeable difference is the apparently complete absence of the "digestive" cells, *i. e.*, those that contain the varicose swollen mycelium. No indications were noted of the destruction of the fungus by the cells of the host and the former is evidently much more nearly a true parasite than is the case in the saprophytic gametophytes. In the infested cells of the green gametophyte the starch and chromatophores are destroyed evidently by the action of the endophyte, but the nucleus remains intact.

Of the ferns with green prothallia, the endophyte has been found, almost without exception, in the following: *Marattia Douglasii* Baker, *Kaulfussia æsculifolia* Bl., *Angiopteris evecta* Hoffm., *Gleichenia* (*Eugleichenia*) *polypodioides* Sm., *G.* (*Mertensia*) *dichotoma* Willd. (=*G. linearis* (Burm.) Bedd), *G.* (*Mertensia*) *lævigata* Hooker, *G.* (*Mertensia*) *pectinata* Presl. In *Osmunda cinnamomea* it appears to be commonly but not always present, and in *O. Claytoniana* it could not be found. The number of slides of the last species examined was not very large and it is possible that further study of this species, as well as of *O. regalis,* will show its further occurrence in the Osmundaceæ.

Of the forms that were examined, that occurring in Osmunda and Gleichenia was the largest (Fig. 3, *B*, *C*) and equal in size to the endophyte of Ophioglossum. The form in Angiopteris was the smallest that was seen.

The Significance of the Endophyte

That the presence of the endophyte is necessary to the existence of all strictly saprophytic gametophytes is indicated by the failure of the germinating spores to develop unless they become associated with the fungus. Moreover, the universal occurrence of a similar endophyte in all humus-saprophytes among the seed plants indicates that in all of these chlorophylless plants the presence of the fungus is necessary for the existence of the host. Although it has not been directly proved, it is generally assumed that one rôle of the endophyte is the elaboration of some of the carbonaceous constituents of the humus. The infrequent communication between the external hyphæ and the internal mycelium makes it unlikely that the nutritive products are directly absorbed by the fungus, and it seems much more probable that the rhizoids of the gametophyte are the direct agents of absorption. How the humus constituents are changed by the action of the fungus so that they are available for

the cells of the host is not clear and it is by no means impossible that some at least of the necessary carbon may be derived from the fungus itself in the digestive process to which it is subjected in the digestive cells. This seems plausible from the fact that in green prothallia, where presumably the plant is entirely able to supply its own carbon compounds through photosynthesis, these digestive cells appear to be wanting; or at any rate they were not observed in the several forms that I have studied. The experiments of Ternetz already referred to showing that certain fungi, including certain endophytic mycorhizæ, have the ability to assimilate free nitrogen, confirms the assumption of earlier authors that the fungus is useful to the host in supplying to it nitrogen compounds; but while this is probably a very important part of its functions, it seems to me that it is not perhaps the only one, and that the necessary carbon is also supplied directly or indirectly through the agency of the fungus.

As Magnus has very graphically shown, the relation of the two symbionts is mutually antagonistic, each one acting as a parasite on the other, but nevertheless the presence of the fungus is essential to the higher organism so long as the latter is destitute of chlorophyl; and the explanation of the wide-spread saprophytism exhibited by so many of the higher plants may be sought in this attempt to defend themselves against what was probably at first a strictly parasitic organism. Having acquired the power to attack and feed upon the parasite, the photosynthetic functions were more and more subordinated until a state of true parasitism (or saprophytism) resulted. The numerous semi-saprophytes like most of the green Ericaceæ and many green Orchidaceæ are good examples of transition stages, while the characteristic leafless humus saprophytes, such as the Monotropeæ and the chlorophylless Orchidaceæ, represent the fully developed phase of this peculiar form of symbiosis.

That this symbiotic association may occur in still lower organisms than the ferns is shown in the familiar case of the lichens, which are most perfect examples of this. It has been shown also that a similar association of fungus and host occurs in a good many liverworts. Cavers[8] has studied this association with some care in the common liverwort Fegatella, as well as in other Hepaticæ. He found in Fegatella that the endophyte is beneficial to the growth of the host, the plant being more vigorous when the fungus was present. He assumed that this was due to the assistance given by the fungus in the assimilation of organic matter from humus or from other organic substrata.

This frequent occurrence of an endophyte in Hepaticæ makes the occurrence of this in the green prothallia of ferns quite readily understood. Whether in the latter it is an advantage to the host to have the endophyte present remains to be seen, but it is highly probable that such is the case. Once having acquired the habit of associating itself with the fungus, the gradual development of the purely saprophytic subterranean gametophytes of the Ophioglossaceæ from green forms similar to those of the Marattiaceæ, is readily conceivable. In the genus Lycopodium there is every degree from the strictly holophytic green prothallium of *L. salakense* to the subterranean chlorophylless gametophyte of *L. clavatum* or the still more specialized gametophyte of *L. phlegmaria*.

Presumably in the Ophioglossaceæ the evolution of the gametophyte has been very much the same as in Lycopodium.

[8] On Saprophytism and Mycorhiza in Hepaticæ. *New Phytologist*, II, 1903.

THE EVOLUTION OF THE TERTIARY MAMMALS, AND THE IMPORTANCE OF THEIR MIGRATIONS[1]

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SECOND PAPER. OLIGOCENE EPOCH[2]

HAVING analyzed the *local evolution* and the *migrations* of the Eocene mammals (*Comptes rendus,* 6 novembre, 1905), I will now consider the corresponding data in regard to the Oligocene.

B. OLIGOCENE FAUNÆ.

I. Lower Oligocene (*Sannoisian* or *Lower Tongrian*). Two successive faunæ:

(*a*) Fauna of the *white marl* of Pantin, Romainville. The fauna of the *lignites of Célas,* Avéjan, Vermeil (Gard), of the limestone of Brunstatt and of Rixheim (Alsace) are probably not very distant from this. Without doubt the same is also true of several deposits in the South West of France: Fronsac and la Grave (Gironde), Sainte-Sabine, Duras, Issigeac, Saint-Cernin (Dordogne). A part of the phosphorites of Quercy,[3] and of the "terrain sidérolithique" of Fronstetten (Suabia) belong to the same level.

1. *Local Evolution.*—Continuance of the Palæotheriidæ (Palæotherium, Plagiolophus), of the Anoplotheridæ (last of Anoplotherium), of the Xiphodontidæ (last Xiphodon), of the Rodentia—Theridomyidæ (Theridomys).

[1] First paper, Eocene Epoch, in the February number of the NATURALIST.

[2] Extract from the *Comptes rendus des séances de l'Académie des Sciences,* t. CXLII, p. 618 (séance du 12 Mars, 1906). Translated by Johanna Kroeber.

[3] The remarkable fauna of the phosphorites is not a homogeneous assemblage, but a composite representing horizons from the Bartonian to the Stampian, inclusive. In general, therefore, I shall consider only those genera of the phosphorites that have been found elsewhere in the stratified deposits, and whose age can thus be positively determined.

2. *No new migration* is known.

This fauna seems to be simply a much-reduced remnant of the Ludian fauna and should be more properly included with the upper Eocene.

(*b*) Fauna of the *limestone of Brie,* of Hempstead (Isle of Wight), of Ronzon (Velay), of Lobsann (Alsace), of Calaf and Tarrega (Catalonia). A part of the phosphorites of Quercy and of the "terrain sidérolithique" (Bohnerz) of Veringendorf, Veringenstadt, of the Eselsberg, of the Hochberg and of Oerlingerthal near Ulm, belong to the same horizon. Possibly the beds of Monte-Promina (Dalmatia) belong to this horizon or to the preceding one.

1. *Local Evolution.*—Continuance of the Palæotheriidæ (Palæotherium, Plagiolophus), of Anthracotheriidæ (continuance of Brachyodus, and appearance of species of Ancodus, some species of *Anthracotherium*), end of the Anoplotheriidæ (last Diplobune), continuance of Cænotheriidæ (Amphimeryx, ? Cænotherium), of Canidæ (Cynodon, Cynodictis, Amphicynodon), of Erinaceidæ (Tetracus), of Theridomyidæ (Theridomys), of Hyænodontidæ (Hyænodon), of the Marsupial Didelphyidæ (Peratherium Amphiperatherium).

2. Important *North American migrations:* Sudden appearance of the Rhinocerotidæ (Ronzotherium), and of the Entelodontidæ (Entelodon).

3. Migrations of *unknown origin* of the Tragulidæ (Gelocus), of Mustelidæ (Proplesictis), of the Myomorph Rodentia (Cricetidæ), and perhaps of the Amphicyoninæ (beds of Tarrega).

II. Middle Oligocene (*Stampian* or *Upper Tongrian*), very numerous deposits: in the Paris basin, la Ferté-Aleps; in Germany, Ufhofen, Flonheim, Miesbach, lignites of Schluchtern, of Gusternheim and of Westerwald; in the basin of l'Allier, *Bournoncle-Saint-Pierre, Bons,* Perrier, Montaigut-le-Blanc, Champeix, Autrac, Saint-Germain-Lembron, Antoingt, Vodable, Solignat, Lamont-

gie, Nonette, *Orsonnette,* Malhat, Les Pradeaux, Les Chauffours, Bansat, Boudes, Chibrac, La Sauvetat, Jussat, Gergovia, Romagnat, Pérignat, Lemdes, Cournon, Marcoin, Chaptuzat, Gannat, Saint-Menoux; in the basin of the Loire, Vaumas, Saint-Pourçain-sur-Bèbre, *Briennon,* Digoin; in the South East of France, Céreste, Manosque, clay of Saint-Henri near Marseilles, *les Milles* near Aix, Auzon near Alais; in the South West of France, Cestayrol, Saint-Sulpice, *Rabastens, hill of Saint-Martin, Montans, Salvagnac, l'Ile d'Albi, Pont-Sainte-Marie,* Tournon, Capellier, Les Péries, *Villebramar,* la Milloque, Comberatière, Moissac, Beauville, Itier, Bourg de Visa, Montségur, etc.; in Switzerland, Blauen, La Conversion, near Lausanne; in Italy, Cadibona in Liguria, Monteviale and Zovencedo in Vicenza; in Austria, Trifail in Styria, and deposits in Dalmatia; lignites of Inca (Island of Majorca); the larger part of the phosphorites.

It seems that from now on it will be possible to distinguish at least two horizons in this important stage: the lower (the principal deposits of which are given in italics in the preceding list), characterized by the persistence of the last representatives of Palæotherium, of Entelodon, or of Gelocus; the upper by the abundance of large-sized Anthracotherium and Acerotherium, and the sudden appearance of the Tapiridæ.

For the stage as a whole, the facts in regard to evolution and migration are as follows:

1. *Local Evolution.* — Continuance of Palæotheriidæ (*last appearance*), of Rhinocerotidæ (Aceratherium, Diceratherium), of Chalicotheriidæ (Schizotherium), of Anthracotheriidæ (Brachyodus, Anthracotherium, several phyla), of Entelodontidæ (last Entelodon), of Suidæ (Propalæochœrus, Palæochœrus), of Cænotheriidæ (Cænotherium, Plesiomeryx), of Tragulidæ (last of Gelocus, Prodremotherium, Lophiomeryx), of Theridomyidæ (Theridomys, Issiodoromys, Archæomys), of Cricetinæ (Cricetodon), of Talpidæ (Geotrypus), of Erinaceidæ (Erinaceus), of Chiroptera (Palæonycteris), of Creodonta (last

Hyænodon and last Pterodon, Dasyurodon), of Canidæ (Amphicyon), of Mustelidæ (Plesictis, Palæogale), of Viverridæ (Amphictis), of Marsupialia (Peratherium).

2. Migrations of *North American origin* of Tapiridæ (Protapirus, Paratapirus), and of Amynodontidæ (Cadurcotherium[4]), and perhaps of the Felidæ-Machærodinæ (Eusmilus).

3. Migration *probably from Africa* (and perhaps a little before the Stampian), of Edentata with normal vertebræ (Leptomanis and Archæorycteropus of the phosphorite beds).[5]

4. Migrations *of unknown origin* of Cervulinæ (Dremotherium, Amphitragulus), of Castoridæ (Steneofiber), of Myogalidæ (Echinogale, Myogale), of Tupaiidæ (Plesiosorex), of Soricidæ (Amphisorex, Sorex), of Lutrinæ (Potamotherium), of the Felidæ-Proælurinæ (Pseudælurus), and of Lagomorph Rodentia (Lagomyidæ, genus Titanomys).

III. Upper Oligocene (*Aquitanian*).

Principal deposits: in the Paris basin, Celles-sur-Cher; in the Bourbonnais, Saint-Gérand-le-Puy, Chaveroche; in Germany, Weissenau and Mombach near Mainz, Haslach, Eckingen near Ulm; in Switzerland the Gray Molasse of Lausanne, Othmarsingen, Hohe Rhonen; in Savoy, Pyrimont-Challonges; in Provence, Varages (Var); Boujac in the basin of Alais; in Catalonia, Rubi near Barcelona; in Bohemia, Tuchoritz; in Karinthia, Keutchach; in Hungary, Waitzen.

1. *Local Evolution.*—Continuance of Tapiridæ (Paratapirus), of Rhinocerotidæ (Aceratherium, Dicerathe-

[4] M. Boule (*Comptes rendus*, 18 mai, 1896) has endeavored to prove an affiliation between Cadurcotherium and certain Ungulata of Patagonia, such as Astrapotherium; this relationship would be interesting, if demonstrated, for it would imply a *Patagonian migration* in the Oligocene period. But the supposed affinity rests, in my opinion, upon rather superficial resemblances of the dental system.

[5] I do not believe in the existence of South American Edentata in the Oligocene of the phosphorite beds. The *Necrodasypus* of Filhol seems to me to be a dermal plate of a Reptile related to *Placosaurus* Gervais.

rium), of Chalicotheriidæ (Macrotherium), of Anthracotheriidæ (Brachyodus, last of Anthracotherium), of Suidæ (Palæochœrus, ? Doliochœrus), of Cænotheriidæ (Cænotherium, Plesiomeryx), of Cervulinæ (last Dremotherium and Amphitragulus), of Theridomyidæ (Theridomys), of Myoxidæ (Myoxus), of Eomyidæ (Rhodanomys), of Sciuridæ (Sciurus), of Castoridæ (Steneofiber), of Lagomorph Rodentia (Titanomys), of Talpidæ (Talpa), of Soricidæ (Sorex), of Erinaceidæ (Palæoerinaceus, Erinaceus), of Canidæ (Amphicynodon, Cephalogale), of Amphicyoninæ (Amphicyon), of Mustelidæ (Stenogale, Plesictis, Palæogale), of Lutrinæ (Potamotherium), of Viverridæ (Amphictis, Herpestes), of Felidæ (Proælurus), of Marsupialia (the last European Didelphyidæ).

2. Smaller migrations *of unknown origin* of the Dimylidæ (Dimylus, Cordylodon).

The Aquitanian fauna is chiefly an impoverished residue of the Stampian.

Important migrations begin again with the Miocene epoch, and these will form the subject of a later paper.

OBSERVATIONS REGARDING THE CONSTANCY OF MUTANTS AND QUESTIONS REGARDING THE ORIGIN OF DISEASE RESISTANCE IN PLANTS [1]

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It is not my purpose to develop a controversy as to theories, but, in pointing out some features of my studies upon disease resistance, it seems necessary to raise some question concerning the rapid development of the mutation theory which I believe to be worthy of close thought before we accept this theory as replacing, in entirety, the doctrine of evolution as formulated by Darwin.

The DeVriesian school has pointed out one way in which plants and animals originate new individuals with characteristics apparently new. The Mendelian formulas, especially as in late years developed, illustrate clearly how apparently new characteristics may appear to be caused to arise. This would seem to be a fair statement of all that has actually been accomplished.

I assent that most of the conceptions arising from the investigations of Mendel and DeVries are probably correct and, after considering expositions depending upon the experiments of many workers and having experimented sufficiently to understand the meaning of "mutants," "unit characters" and "elementary species," I recognize that these works added much light upon how evolution in plant life takes place, and that henceforth the conception of unit characters must largely form the theoretical working basis for practical breeding work. Yet I feel sure that Darwin's conception was sufficiently broad to embody both features as minor parts of the great concept of organic development. To accept De-

[1] Read before the American Breeders' Association, Washington, D. C., January 29, 1908.

Vries' doctrine of mutation as a substitution for the Darwinian conception is, I believe, to accept a part for the whole and to place before the farmer and stockman a doctrine which, if generally accepted as a substitute for the broad conception of Darwin, can not but be narrowing and injurious.

DeVriesian and Mendelian phraseology, in daily use, may be to blame, but in reading many of the late expositions one is led to question whether the doctrine of constancy of elementary species or constancy of unit characters can be accepted by biologists and breeders with any less damage to after progress than that which followed the once complacent acceptance of the Linnæan dogma of the constancy of species.

DeVries, of course, argues for the acceptance of the validity of evolution by mutations, and while one may readily concur that such mutations occur, one who works largely with cereal crops and has always recognized that the individual is the proper starting point for selection work, is apt to be astonished in reading his new work on "Plant Breeding," and falls to questioning whether after all, a mutation may not be merely a "fluctuating variation," big enough and stable enough to be recognized. Is it possible that the nature of these changes is different in kind or only in quantity and range of duration? Does accident play so large a part in plant development and plant breeding as indicated by most DeVriesian writers? One need not object because of the wonderful things said of elementary species, for good Darwinians have always believed in the existence of strains and subspecies which would admit of the name; nor should we expect any less of DeVries than that he should use the arguments related in "Nilson's Discovery" and those from such other experiments and expositions as would, when handled in certain lights, tend to show evolution by mutation. Yet, one who recognizes all of the possible merits that accrue from the conception of hypothetical unit characters and of the existence

of plant strains which admit of the designation "Elementary Species" may be pardoned if he is unable to accept another dogma of constancy, and is unable to subscribe to many DeVriesian conclusions regarding the comparative merits of mutation as opposed to adaptation and natural survival. Most of us, I believe, can only look upon a mutation as one of the types of variation through which the survival process brings about evolution. I believe that we still have to look for the underlying causes. An ardent Darwinian can well agree to the statement: "Species are derived from other species by means of sudden small changes which, in some instances, may scarcely be perceptible to the inexperienced eye,"[2] but may find points of doubt and refuse to follow to the limit when reading a number of statements found in the same work, for example, "From their first appearance they are uniform and constant."[3] This statement refers to species. Again, "The conception of mutations agrees with the old view of the constancy of species. This theory assumes that a species has its birth, its lifetime, and its death, even as an individual, and that throughout its life it remains one and the same."[4] "Each single type (be it species or subspecies or variety) is thus wholly constant from its first appearance and until the time it disappears either after or without the production of daughter species."[5] This last sentence is certainly clear to the effect that a species is never changed, at least so as to affect its after progeny. It is equivalent to saying that all individuals after formation in the seed remain exactly like the parents and, taken with the other statements which insist that plants mutate, means that they remain constant until they change, which is an absurdity in argument. With this, we must assume that a man can recognize ultimate unit characters and can recognize just how many characters it takes to make a species. When

[2] DeVries. Plant Breeding. Page 9.

[3] *Ibid.*, page 9.

[4] *Ibid.*, page 8.

[5] *Ibid.*, page 9.

we can do this, there will not be any use for the Breeders' Association. "... Mutations occur constantly, without preparation and without intermediates."[6] I can not think of a mutation or change in species occurring without preparation and without intermediates. It is equivalent to saying without cause. Later, one reads, "We may confidently assume that each single mutation affects only a single unit."[7] I would certainly agree with this statement if I could conclude from the author's other statements that he had in mind that a plant might be made up of an inconceivable number of unit characters, the ultimate nature of which may, after all, be only matters of force. "In other words, the principle of adaptation, as one of the main parts of the theory of evolution, should be separated from the study of the geographical distribution. . . ."[8] As to this assertion, I agree that plants migrate and select in the same sense that men migrate and select, but I can not agree that a species never adapts itself in such form as to transmit the results of adaptability.

"Environment has only selected the suitable forms from among the throng and has no relation whatever to their origin."[9] "Natural selection . . . causes survival of the fittest; but it is not the survival of the fittest of individuals, but that of the fittest species, by which it guides the development of the animal and vegetable kingdoms."[10]

These last two quotations contain sweeping assumptions and all of them taken together must be interpreted as saying that evolution in plant and animal life arises wholly from accidental changes, that is, from mutations which are matters of accident, having no preceding cause, therefore beyond us as breeders to investigate or change. This would naturally deprive agriculturalists

[6] DeVries. Plant Breeding. Page 24.

[7] *Ibid.*, page 322.

[8] *Ibid.*, page 345.

[9] *Ibid.*, page 352.

[10] *Ibid.*, page 9.

and stockmen of the right to hope for the adjustment of a species to new surroundings in which at first it does not fit.

It is hard to comprehend a philosophy which recognizes the old conception of species yet breaks it into countless "elementary species," and at the same time claims absolute constancy for the characters of the elementary forms. If mutations, which all agree may occur, do not come from irritations of environment, internal or external, from what cause may they arise? Must we say that each plant with an observable unit character is a species and, with Linnæus, that it always was? My observations do not allow of this thought; neither have I ever seen an accident in nature. The only observed accidents of nature, when known, have always been found to have direct natural causes. I could not work with faith upon plant breeding if I could convince myself that any plant was ever the result of an accident.

The fact that plants mutate and that new types arise in regular mathematical relations due to cross breeding, and that selections from individuals give the correct methods of breeding, seems evident, but I have seen nothing to convince me of absolute constancy of either individual or species. Mutation seems to be just a good name for a grade of natural changes and no more. We have still to look for the causative feature in the environment behind the mutation or change of character; and, if we wish to improve upon agricultural species or varieties or individual strains, we must select from among the occurring changes, whether we call them mutants, elementary species or unit characters. The demonstrations of mutations and the new knowledge that arises from a better understanding of the laws governing union of and correlation of characters must eventually greatly facilitate the studies looking toward an understanding of direct special causes for the changes which occur in the evolution of a type. DeVries' original experiments were of immense value, but I believe his philosophy of constancy to be

exceedingly bad. There seems to be no observation or experiments which can be interpreted as substantiating that phase of his writings. While DeVries' examples all point to the minutest types of variation and change, his philosophy of constancy is directly opposed to this thought and would dash all of the hopes of the average man doing any work looking toward the improvement of strains, or types. Yet, previous to the last few years, since college men have been given sufficient funds for experiment, it was the practical farmer and stockman who had done the work in improvement of agricultural sorts and races in stock, and most of the improvements have been made from pedigreed strains of rather pure type whether we speak of vegetables, fruits, cereals or cattle. I know this statement will meet with objections, but I believe it will be found to stand upon good bases when we remember the work of our horticulturists and best breeders of animals. For example, Wellman, Haynes and Houston used plant gardens for the production of individuals from individual mother plants in wheat before De Vries, Nilson or Hayes worked. I can not convince myself, after studying the results and observing the work of Mr. Haynes in later years, that he or the other two men got results only from their first selections. Each of these men have time over and again told me that they selected only the best strains from the progeny of the best individual and that each year their crop had improved in the direction along which they worked and that it maintained itself reasonably well in the field. This, of course, DeVries would answer was only the result of "fluctuating variations." My studies do not convince me that he is correct. Undoubtedly, there are countless variations which may occur in the field crop which it is folly to assume may be detected and classified as permanent or fluctuating. Certain it is, that Darwin argued for the great stability of certain inbred stocks and that forces of heredity are stronger than those of variation. It is equally true that the longest pursued

experiments of American agriculture show that pure strains or varieties of close-bred stocks, especially those of cereals, are sufficiently stable to be held to form under intelligent culture, but none of us, as yet, can say further than this. If we maintain and can agree that a mutation or change has a natural cause and that no plants are stable, constant in character, it is nevertheless not necessary to be assumed that the burden of proof rests entirely upon Darwinians.

What evidence may be placed over against the theory of constant elementary species? Well, as an hypothesis, when carried to the limit, an elementary species becomes a unit character and when unit characters are well known they will as in the case of the units of matter, perhaps become so intelligible as to be recognized as the least conceivable element of natural force which makes for union and which in case of the organic units may make for a heritable change. This, the writer believes, is the ultimate result to which most of DeVries' facts and observations point, and my own observations, together with those of others, as I undestand them, teach that whenever physical and chemical conditions are changed in the least, within or without the plant, some variation will occur in plant substance, and that this may result in a change in the progeny which may be fixed or modified sufficiently to serve agricultural purposes, if the conditions which originate it may be ascertained and reasonably maintained. It is but reasonable that some changes should approach greater stability than others.

The practical breeders of America, years before the work at Amsterdam and Svalof commenced, developed hundreds of varieties; and though I have worked with many varieties and strains of wheat, flax and potatoes and have found them all reasonably stable if given generally stable environment, I have never yet been sure that I have seen a stable plant or stable strain or variety. Some change is continually taking place and any change, I think, may be fixed just in proportion as we know the conditions which originate it.

This brings me to the statement of a principle of agricultural cropping which, though generally recognized by breeders for years, yet needs to be much emphasized by those who would improve a character of a plant or a plant strain, or maintain a standard of a general crop; namely, the condition under which a character originated or is being originated must be maintained or approached. It is all the more important to hold this feature of cropping well in mind, now that the conception of unit characters and of mutations and of new methods of experimental breeding has proved to be of such fertile aid in the production of new types. Much of the value of agricultural, commercial cropping rests upon the permanence and general use of a few well-maintained or established varieties as against the miscellaneous use of many varieties; thus, for instance, a district or country gains its reputation for a particular crop not by the use of many varieties, as, for example, of wheat, or oranges, but by the use of a few which by careful work are held to their characteristic qualities. It is quite possible to swamp agriculture by the creation of too many forms. Stable industries are built up about reasonably stable crops.

After a new type or a new character in a type has been obtained, new conditions, if they include the essentials of the old conditions, may readily bring about the addition of new features whether we have in mind calling these new features fluctuating or elementary. If the originating conditions are lost or are not maintained, the type should degenerate or retrograde, lose character, and I am quite convinced that it always does. Herein lies the working basis for every-day cropping and breeding. This line of argument is equivalent to saying that so-called fluctuating variations may be maintained and built upon as foundations for important hereditary changes, whether, in writing, we term the resultants mutants, sports or simply elementary units or species. It is equivalent to arguing that the principle of adaptation may

be active in nature even though mutations are observed. Or, perhaps plainer, it is equivalent to saying that mutations themselves may be nothing more or less than adaptations, adaptive changes. I think breeders who ignore this thought in their work will eventually find themselves without a basis for well-founded experiments.

I have been brought to these conclusions chiefly through careful observations upon my own selection and breeding plots, upon which for a number of years, I have attempted to hasten the survival of the fittest, or of the unlike, through the development of or heightening of the action of plant disease for the purpose of eliminating the weak or unfit.[11] The method of field work consists essentially in constant culture or cropping to the crop under consideration and in promoting, in every way possible, the development and action of the disease under consideration; and at the same time using all available methods of breeding and selection under these heightened conditions of disease. The method has given marked results when applied to wheat *vs.* wheat rust; wheat *vs.* wheat smut; flax *vs.* flax rusts; flax *vs.* flax wilt; and potatoes *vs.* scab and blight.

My observations along these lines have been such that I have no fear but that the future will find me right in the assertion (1) that mutants may be so insignificant and numerous as to be unrecognizable and thus fall directly into the class called by DeVries, "fluctuating variations"; or (2) that they may be induced in a mixture of a great number of varieties of a species at one and the same time because of the same environmental causes; or (3) that, in some cases, "fluctuating variations" are of such nature and worth as to allow results to be obtained

[11] The full details of the methods and details of the results can not be furnished in the limits of this paper. The method of work has been outlined in the annual reports of the North Dakota Agricultural Experiment Station and in an address delivered before the meeting of farmers and stockmen at St. Louis, October, 1903, and further reported upon in vol. I, page 131 of the report of this association, and also in the Proceedings of the Lansing Meeting of the Society for Promotion of Agricultural Science, p. 107, 1907.

in mass breeding of as great importance as any that may be hoped to be obtained by looking for a single mutating type evolved through the method of DeVries.

I am unable to affirm whether disease resistance, immunity to disease, is structural or physiological. I believe the latter, for I have been able to develop it in varying degrees of perfection in every strain of potatoes, wheat or flax with which I have worked, and for all of the diseases noted, while the method used has always remained the same. There is also good structural evidence that it is physiological, as shown in the structural changes caused by the entrance of disease-producing organisms within the tissues of resistant hosts. I have worked with pure strains, centgener progeny, from individuals, with the progeny of cross bred plants, with mixed strains and variations in bulk, and with bulk selections of centgener origin, side by side, and resistance has come at approximately the same rate and grade for a variety through any one of these methods. When the conditions of disease production and conditions of infection for each plant have been held so as to be constant factors, the bulk method of selection, as, for example, selection to seed weight, color and form from a disease plot of flax, has given final hereditary resistance as rapidly as individual selections from the progeny of individuals of the same strains. The only cases in which resistance has developed irregularly in such strains of flax or wheat have been found to be due to impurity of type or to irregularities as to the constancy and amount of disease infection, or to irregularities in the conditions promoting the development of disease.

Resistance to the diseases named for the crops named can be developed in any variety or strain by either method of selection noted. In any case, it may be increased by every proper selection year by year, just in proportion to the perfection with which the disease conditions of elimination are maintained.

The method works in potato selection, where the process

of propagation is by cuttings or buds and hence only a condensed individual life. It works in wheat, which seems quite guarded in its closed or individual fertilization. And it works in flax which, though usually self-fertilized, is, no doubt, much given to intercrossing in the open.

If the proofs rested only upon flax, where there are many possibilities that open crossing might give rise to the various Mendelian types, homozygotes, heterozygotes, etc., the evidence might be thought to be thrown into question, but even there, when crossing is promoted, while there is every evidence of the occurrence of resistant or non-resistant types among the crosses, resistance is seldom found to approach the immune type upon the first possible selection. In other words, if mutants do occur in flax through natural crossing or self-fertilization, so far as our experiments are concerned, these resistant forms are found to act exactly as do those which may be developed from ordinary types of non-resistant flax.

With this crop, one finds little, if any, resistance to wilt and to rust in the best seed strains of southern Russia or in the best seed strains from the new lands of our northwest or in the best fiber strains of the disease-free districts of northwestern Russia, though it often crops out in the general seed samples from the worst disease infection regions of central Russia. If mutants were without cause and constant, one ought to find them as readily in the seed of one district as in another. One can, however, build resistance upon the least resistant of these strains, if the work is started upon a graded scale of disease infection which is increased year by year. If the seed is placed under too heavy conditions of wilt production, the plants are all killed in embryo or young stages of growth and nothing is gained. If, however, scrubs or runts may be saved from the first season under weak disease infection and a graded infection is followed thereafter, in approximately five years one may bring these strains of seed to such a stage of resistance that ordinary agricultural methods of cropping will maintain

them upon the most flax-sick areas. But whether these resistant strains have been selected through crossing or by this gradation method from bulk seed or from individuals taken from a known pure strain, I have found that abrupt heightening of disease conditions of too great violence may undo the whole work.

It holds as well for wheat when speaking of rust attacks. Under uniform conditions of rust infection, all wheats arise rapidly to a stage of marked resistance to general uredospore infection whether caused by the type *Puccinia graminus* or *P. rugigo-vera,* which resistance seems to be characteristic for each variety concerned, but may then fall a ready prey to sudden attacks introduced by properly conducted aecidial infection. All this points to the rôle played by the irritations of environment, which either govern the appearance of mutations or produce other changes which are very worthy of the breeders' and croppers' attention; and allows one to ascribe much more merit to methods of mass selection and breeding in cereals than the DeVriesian doctrine of constancy of elementary species will allow one to assume.

No phase in this argument touches upon the ultimate causes of disease resistance or immunity. But the facts do point quite clearly to the probable influence of chemical agencies, perhaps toxines, arising from the direct existence of fungus attacks upon the hosts. In my mind, there is not the slightest doubt but such attacks originate heritable resistance, in much the same sense as MacDougal's chemical injections upon ovaries are supposed to have originated new types. If later experiments prove MacDougal's observations to be well founded, the results will be of far reaching importance. If these suppositions that fungus attacks upon the host may induce fungus-resistant qualities in the progeny from the matured ovaries, are correct, no doubt the unit characters, so called (whether simple and definite in number or whether they may be considered as composed of countless and variable elements of the cromatin structures) may be effected, or

may be originated, and one ought, under crossing, to observe the effects in terms of dominant and recessive or cloaked features. Such effects I have observed to occur in flax as against flax wilt and in wheat as against *P. graminus.* Mr. R. H. Biffin, of England, is reported as indicating that this is true in the case of wheat when crossed with eincorn as against yellow rust.

Bateson, in an admirable article upon "Facts Limiting the Theory of Heredity,"[12] would also seem to enroll himself as against any adaptative response to changed conditions as able to account for the origin of such facts as I have observed in my cultures of flax and wheat. Thus we read:

> "Though the response to change of conditions may have been direct, it must not be hastily concluded that the response is adaptive. The appeal to direct responses so common in evolutionary discussions of thirty years ago, was made to account for the complex adaptations of organism to environment. It is the total want of any evidence supporting that appeal which has driven most of us to disbelieve in the reality of any such claims, and there is nothing in the new evidence, I think, which should shake the attitude of resolute agnosticism which we have thus been led to adopt."

However, to explain such observations as those noted by me in the flax and wheat cultures seems to demand the assumption that additional elements of heritable character arise on account of causes demanding adaptive response. No theory of quantitative subtractions of unit characters already formed would seem to be adequate to account for the observed acquired qualities of resistance. It is probable that only the cytologists are in position to produce direct proof or disproof of the apparently necessary suppositions as to character modifications. Certainly those among them who are experimentally inclined may cut along the line indicated with much hope of uncovering many high lights to breeders. Even here, it may be expecting quite too much that possibly pure physiological qualities should be represented by structural units.

[12] *Science,* November 15, page 649.

WHAT IS A SPECIES?[1]

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WE have had in the past not a few interesting discussions upon or controversies over the methods of evolution and the origin of species in this club. We have more or less plausible theories as to the evolution of species, by natural selection, mutation, inheritance of acquired characters, etc., but we have very nebulous ideas as to what species really are. Nothing is more common than the term species; nothing is more uncertain than what species are.

Long after the present topic had been suggested for discussion by the club, I was delighted to learn of a like discussion to be held at the late meeting of the Botanical Society in Chicago. I anticipated that symposium with the liveliest feelings of satisfaction, confidently expecting a brilliant illumination of the whole umbrageous subject, an effulgence of light that would throw into deepest obscurity whatever feeble beams I might myself hope later to cast upon it. But lamentable was my disappointment. I heard some ancient platitudes that the zoologists ceased in despair to consider a dozen years agone, and many anathemas showered upon the botanical taxonomist. They berated him for making such a mess of classification, and hinted very freely that he didn't know much anyhow, and probably never would. If all that was said be true, then indeed the botanical taxonomists are a sorry lot. One distinguished speaker declared they had made no progress since the time of Linné, and he rather seemed to desire that the whole tribe might be banished to some desert isle where there is neither vegetable life nor printer's ink, that they might no longer trouble the ecolo-

[1] A paper read before the Biological Club of the University of Chicago.

gists and physiologists, *et id genus omne.* But I can not escape a harrowing doubt as to what the learned speakers' vocations in botany would be, if the maligned taxonomists had not got in their diabolical work. Possibly they would distribute an herbarium with each lucubration, that their readers might know what they were writing about; or possibly they might undertake to name their own species, for I have seldom known the morphologists to escape the mihi itch on very slight infection.

I sympathize with the physiologist or ecologist, who after he has written a luminous paper on a Cratægus or Viola, or Rosa, or Opuntia, endeavors to ascertain the proper name for his plant; but I do not sympathize with his objurgations against the whole tribe of species makers. There is a deal of pseudo science, unripe science—were it not undignified I would characterize some of it by an expressive monosyllabic word suggesting decomposition —published about species by the taxonomists, but I suspect that there is also a large deal of like obnoxious material lying at the doors of the physiologists and ecologists and morphologists. But that fact does not make taxonomy or ecology anything less of a science, nor the work of able men in either less valuable. I am a little weary of hearing from narrow specialists in other departments of biology constant condemnation of the taxonomist, and I have been hearing such for the past fifteen years from men who should know better.

Now, as one who has been guilty in the past twenty-five years, let me say it humbly, of naming and attempting to describe ten or twelve hundred so-called species and genera, I beg leave to make a few remarks about species. You may properly accuse me of being one of those degenerates the taxonomists and, as his tribe is not well represented here to-night, I may be permitted to present his side of the case. I hold no brief for the criminals, but, as one of the accused, I would present my own defense and my own views.

The question, What is a species? has been asked re-

peatedly, I may say continuously, since the time of Linné, even if our friends the botanists have been somewhat somnolent of late. We have had no satisfactory answer, for the simple and very good reason that there is none, and never will be. If we could go back to the happy Cuvierian or even Agassizian days and throw the whole responsibility of their definition upon the Creator, seeking some revelation in Holy Writ, it would save us much useless worry. But, as we have long since learned that species, like Topsy, just grew, we have and always shall have as great difficulty in deciding when varieties and races become species as we have in determining when a puppy becomes a dog or a lamb a sheep.

Let me premise further with the statement that true taxonomy is the most advanced and difficult of all biological science. O modest claim is it not? But I think that you will readily admit that evolution, as a science, is the highest end of biology—and taxonomy is merely the graphical expression of evolution. If, then, we do sometimes baptize a score of hawthorns, or bedbugs, or coyotes, where the breeder or ecologist thinks that he finds but one later, we crave your sympathy and your aid, not your scorn and contumely. The breeder may get all variations between the domestic ox and the American bison, and they will breed reasonably true by artificial selection, but the assertion that *Bos americanus* and *Bos taurus* are one and the same species would be preposterous. Is it not possible that some of our learned breeders of plants and animals may be in error themselves in their views of "species"?

All classificatory terms are impossible of exact definition. Their use always has and always will depend upon the consensus of opinion of those best qualified by wisdom, experience and natural good sense. They will never become stable; we shall never cease to amend, to change, to repudiate old and propose new, because we shall never reach the final summation of science. We can only hope that all changes shall be for the better, shall be nearer the

real truth; that incompetent and inexperienced taxonomists shall be ruled out of court, even as incompetent anatomists and cytologists are disbarred. The unfortunate thing is that we taxonomists have so bound ourselves in a snarl of laws and by-laws that we are compelled to incubate and wet-nurse every premature and monstrous taxonomical imbecility till it dies a natural death, whereas those of other biologists are promptly strangled or thrown out into the cold to die of inanition. Let us hope that we may escape from some of that snarl, or at least that we may cut some of the bonds which hold us too tightly.

To discuss our subject in all its details and bearings and from all view-points would require, not one evening, but many. Permit me, therefore, to offer for your consideration certain axioms of evolution—theories or hypotheses if you prefer to call them such—bearing more or less closely upon the question, What is a species? Some or all may be familiar to you—I do not know whether all have beeen in print or not—but, such as they are, they are all based upon my own observation, and, so far as that goes, I am prepared to defend them, and will endeavor to do so later if there are any you repudiate, as perhaps there are.

1. The only biological entity is the individual, and the individual is inconstant.

2. The value of specific characters is dependent upon a number of interrelated and inseparable factors, the chief of which are environment and heredity.

3. Accumulated heredity may outweigh natural selection or environment, and *vice versa*.

4. A crescent phylum is more variable, more plastic than a long established one; that is, time is always an element in the fixation of characters and the limitation of variation, and the length of time is dependent more or less upon the strenuousness of environment and selection, and the plasticity of the type.

5. New phyla arise from crescent phyla, never from decadent or even dominant ones.

6. The decadent phylum may present as unstable saltations, generic or even higher characters of allied dominant groups; that is a character of generic or even family value in a dominant group may be merely an individual variation in a decadent one.

7. The members of a dominant group are, *ceteris paribus,* more closely adapted to their environment, their characters less variable, their geographical distribution more restricted. That is, species of dominant groups may be safely based upon less distinctive characters than those of a crescent phylum.

8. It follows that senility and decadence are the attributes of species, families and orders, as well as of the individual.

9. The older the genus or allied group of species, the more restricted, apparently, is fertile hybridity. For example: The genus Rhinoceros is an old one that has been but little modified since early Miocene times; I have never learned of cases of hybridity between living species. Equus arose in early Pliocene times with all its essential modern characters; hybridization between all its living species is not difficult, but the hybrids are infertile. The genus Bos, while beginning in the Pliocene, did not attain full development till Pleistocene times; its numerous species are continuously fertile in all combinations. Rhinoceros is long past the zenith of its evolution; its highest specialization was in the Pliocene, or at most Pleistocene. Equus, too, is past the highest point of its development, perhaps, but not far. Bos, on the other hand, is a dominant or crescent type; its maximum specialization is in the present time.

10. Secondary sexual characters are transmitted to the opposite sex, unless of positive disadvantage. Varietal and specific characters, in the natural course of events, are more or less unisexual at their inception, and the constant tendency is for the characters of one parent to be transmitted to offspring of both sexes, even when such characters are apparently useless, as seen in the rudi-

mentary mammæ of the human male, which, indeed, sometimes become of functional use.

11. Secondary sexual characters are more numerous and less stable in the male than in the female; that is, female sexual characters, whether primary or secondary, may be of generic or even family value in groups wherein like characters in the male are merely specific or even individual. I am aware that some modern naturalists would discredit sexual selection, but, until some hypothesis is given to replace it, I must still continue to believe that sexual selection is necessary to account for secondary sexual characters.

12. An organ once functionally lost is never permanently regained by natural selection or any of its hypothetical substitutes. A hexadactyl species of Homo or Felis is impossible.

13. Giantism in any group is an indication of approaching decadence; giants never give origin to dominant phyla of smaller average size.

To these I may add, as an article of faith, one more:

14. Fertility depends chiefly upon the inheritance of physiological characters. A modification in the behavior of the sperm and germ cells may affect fertility even before structural characters have become much affected, and *vice versa*. Human males and females, as we all know, are sometimes infertile with each other, though each may be entirely fertile with some other; an extension of this infertility to races would produce what the taxonomist would accept as species. I furthermore believe that the accumulated inheritance of physiological characters may and does produce determinate lines of evolution, that is, orthogenesis, which may go on into hypergenesis, if I may use this term to indicate that hereditary momentum which results in over-development of organs. I account for this accumulated heredity by the action of past environment upon the organism, that is, Lamarckism. I am also quite aware that I am with the minority in the acceptance of Lamarckism as the chief causative prin-

ciple of the origin of species. I am told that the direct effect of environment in modifying germ characters can not be proven, and I retort, neither can it be disproven. Paleontologists almost universally, and taxonomists generally, are Lamarckians, that is, those who deal chiefly with range and distribution, time and space; laboratory biologists, on the other hand, are almost invariably opposed to the theory of the transmissibility of acquired characters. We can see no alternative hypothesis that will meet the requirements of the classificationist or the paleontologist, and we respectfully submit that the experiments of a few years or even scores of years are trivial in comparison with the natural experiments that go on through tens of thousands of years in the origin and fixation of species. From my little water-garden some years ago I took some plants of the common water hyacinth and planted them in the ground. I was surprised to find that they grew luxuriantly, but that they did not develop the peculiar bladder-like swelling of the leaf stems; when I again transferred some small offshoots to the water, they promptly redeveloped them. The plants immediately changed their structure in adaptation to their terrestrial or aquatic environments, and doubtless they would do so after many years of isolation. But had the water hyacinth been cultivated as a garden plant in the soil since the time of Pliny I believe that the terrestrial character would have become fixed, and, after all, two or three thousand years is a very short time in the history of plant species. The Weismannians have been compelled to recede a long way from their first position of the absolute and eternal distinction between germ-plasm and body-plasm; perhaps we shall yet find an intermediate place that will satisfy us all.

In claiming a high degree of importance for physiological characters and physiological isolation in the formation and preservation of species I need not say that the term physiological is merely a confession of ignorance. All physiological function must inevitably depend ulti-

mately upon structure. Two cells absolutely alike must doubtless function quite alike. But I doubt if there ever are any two cells *quite* alike. We are already learning, if I am correct in my understanding of the claims of McClung and others, that even minor, so-called specific differences are discoverable in the cell, in some groups at least. There is, of course, no such thing as a purely physiological species, for changed structure must underlie all variation, though we may not be able to discover the differences. I can conceive that additional or modified chromosomes in the germ cells of the greyhound might indicate a partial physiological isolation which has preserved this race of dogs almost undefiled through more than three thousand years; certainly man has not been the cause of its preservation.

Now, if the foregoing theses or hypotheses be true, or even if the greater part of them be fundamental principles of variation, it follows that the definition of species must be made for each and every one that exists or has existed; that a specific character in one group may be merely varietal in an allied group, on one hand, or generic in another, on the other hand. Or, aphoristically, every species, as we know to be the case with every genus, is a law unto itself. And this is, practically, the working rule of every competent taxonomist, though of course many sad errors are made in its application. And it follows that he who is best qualified to propose and name species, or to criticize those which have been proposed by others, is one whose acquaintance is widest with living forms and with the laws which underlie their evolution. He must not confound genetic with adaptive characters, for phylogeny is the sole end of taxonomy.

Since we can not give an answer to the question, What is a species? let us analyze briefly some definitions of the past:

1. A species is a form of life which breeds true to itself. The Jewish race has bred true to itself, as indicated by its distinctive physiognomy, since the time of Rameses; and

the Bourbon nose is characteristic of that family. Ergo, the Jews and the Bonapartes are distinct species of Homo!

2. True species are incapable of fertile hybridity. The example of the Catalo, the fertile hybrid between *Bos americanus* and *Bos taurus,* will suffice. The domestic dog interbreeds freely on the plains with the coyote, and no one doubts the specific validity of *Canis latrans,* whatever we may think about coyotes in general. The domestic cat, according to Pocock, is a hybrid between the wild cat of England and the wild cat of Egypt, with a distinct tendency to vary along ancestral lines after centuries of fertile hybridity. The domestic races of dog freely interbreed, and yet we are quite sure they are the derivatives of several wild species of Canis. May not fertility, as a physiological inheritance, account for the preservation of their distinctive types, notwithstanding man's artificial selection? Is it probable, for instance, that the Boston terrier hybrid will continue longer than the fad of its breeding remains undiminished?

3. A species is a type which varies only within narrow limits. The jungle fowl is fairly constant in nature. Its extraordinary variability is seen in the domestic fowls, whether they be derived from a single or several wild species. And the doves are still better examples. A turkey and guinea-fowl, on the other hand, though they have been domesticated for centuries, vary but little from their ancestral types.

There are other definitions. But, you say, if I accept no definition of species what rules do the taxonomists have who "make" so many thousands of them? We must have some, and we do have them, even if we are so often accused of depending on whim and imagination. And these are mine: Forms of animals which present distinct assemblages of characters, in form, color and arrangements of parts under natural conditions, which are recognizable from descriptions and figures, should receive distinctive names and be catalogued, provided, of course that the assemblage of characters includes all onto-

genetic changes. If, in the examination of abundant material from different natural environments, we find these characters fairly constant, the forms may properly be called species; if not, varieties or races. No perfect specific description can be drawn from a single specimen or from a few even, and the skill of the taxonomist is conspicuously shown in his ability to distinguish between variable and fixed characters, between the essential and non-essential, in other words, between old and new characters. Some taxonomists—and I know such—remain, after many years' experience, unable to dissociate individual from specific or generic characters; they describe species as they would describe the physical features of a tree or of a rock—and they are the ones who deserve the condemnation of other workers. Are such workers confined exclusively to our branch of biology?

In nature the interrelated factors, of which environment and heredity are the chief, are normally in a state of substable equilibrium—variations within given groups are within certain fairly definite limits, because the factors of variation are. If, however, the cumulation of any one factor, either naturally or artificially, occurs, the variations become inconstant and the limits of variation are changed. The wild pigeon in nature, for instance, is governed by fairly constant conditions, and its variations are small. Its domestic varieties, were they existent in nature, would not interbreed, and would be good species. Breeders, I think, lose sight of such things when they say, as some do, that they can produce specific characters, that is, characters which are deemed of specific value by taxonomists. They can do nothing of the sort. You may break down by changed environments and artificial selection what would be real specific characters under natural selection and natural environment, but you do not make species thereby. Time and fixation by heredity, I believe, must always be taken into account in determining varietal, specific or generic characters. Mutations of *Œnothera lamarckiana* were found growing wild by de Vries, es-

caped from some garden. Under cultivation he continued to breed them, and produced others. But his plants were all under abnormal environments. Dr. Lutz, whom we all know, is doing some exceedingly interesting experiments upon certain small flies, *Drosophila ampelophila.* He has produced some remarkable sports or "mutations," and the surprising thing is that he finds that such sports breed true, that there is an apparent loss of fertility between them and the normal forms. But I think it is absolutely certain—and I speak as an entomologist fairly familiar with flies—that it would be impossible to produce species of his sports, even though they were bred for a thousand years. As some of us know, polydactyl cats are rather abundant in some parts of Connecticut, breeding true—but who believes in a species of six-toed cats? It is rather unfortunate that breeders confine their attention almost exclusively to plastic forms, that is, to geologically recent types. Let some one try experiments with archaic forms and watch the results.

Experimental breeding and ecology are the two fields of biological research which promise most at present; they will doubtless contribute not a little to our knowledge of the methods of evolution, and correct not a few errors in taxonomy; but I say, with full deliberation, that experimental breeding without a wide knowledge of taxonomy will lead to false conclusions and be comparatively barren of results. The experimentalist, of all men, must be well acquainted with varietal specific and generic characters in the groups which he studies, or he will be working blindly. And I am sorry also to say that some of the severest criticisms of taxonomists and taxonomy have come from some of these men.

SHORTER ARTICLES AND CORRESPONDENCE

THE INHERITANCE OF THE MANNER OF CLASPING THE HANDS

If the hands be clasped naturally, most people will put the same thumb—either that of the right or of the left hand—uppermost every time. The position assumed apparently has no relation to right- or left-handedness, although, as will be shown, a small majority put the right thumb uppermost. Some time ago letters were sent out asking for data concerning the manner in which the different members of families clasped their hands. Among the many generous replies was one from Professor J. Arthur Thomson, of Aberdeen, Scotland, giving data for about 600 individuals. It was intended that the hands should be clasped with the fingers of each hand alternating; but this was not made as clear as it should have been, and some of the correspondents clasped their hand with all of the fingers of one hand between the thumb and index finger of the other. This confusion does not exist in Professor Thomson's data. Accordingly only they are discussed in this note. The accompanying table gives a condensed analysis of the data, R and L standing for right thumb uppermost and left thumb uppermost, respectively.

Parents.	No. of Families.	Offspring.					
		Male.		Female.		Total.	
		R.	L.	R.	L.	R.	L.
♂ R. × ♀ R.	75	71	23	95	40	166 (72.5%)	63
♂ R. × ♀ L.	49	33	22	28	27	61 (55.5%)	49
♂ L. × ♀ R.	53	46	24	40	40	86 (57.3%)	64
♂ L. × ♀ L.	36	24	29	22	34	46 (42.2%)	63

It is evident that the mode of clasping the hands is inherited. It can scarcely be acquired by imitation as it is too slight a thing to be noted unless attention is called to it. The thumb position is usually quite constant in very young children. However, it does not seem to follow the Mendelian law, as neither position breeds true. The data show no significant sexual dimorphism,

61 per cent. of the males having the right uppermost and 58 per cent. of the females; 59 per cent. of the parents and 60 per cent. of the offspring put the right uppermost, so that there does not appear to be any reproductive selection. The coefficient of association between parents of 0.02 demonstrates the lack of assortative mating. This last conclusion is in sharp contrast with the results concerning other characters in man.

There are a number of somewhat similar problems in the lower animals which are of importance in the study of evolution. Thus, the males of the common black cricket (Gryllus) usually keep the right tegmen over the left. This results in one set of sound-producing organs being functionless. In the closely related Locustidæ there is only one set of sound producing organs and the tegminal position is fixed. It would be interesting to know if mutations to the other position occur. The fish *Anableps anableps* has the anal fin modified into an intromittent organ adapted for sidewise motion. On about three fifths of the males it can move to the right and on about two fifths to the left. (AMER. NAT., xxix, pp. 1012–1014.) A similar state of affairs exists in the females, but with the relative frequencies reversed. Copulation is effected by a right male at the left side of a left female and *vice versa*. Whether the species will eventually split up into two on the basis of this character or not would seem to depend on how the anal-fin-twist is inherited. However, if the tendency to twist to the right or to the left be inherited as a character apart from sex there would seem to be no chance of two varieties or species being formed, as each mating is between opposites. The reversed position of the nerves in the optic chiasma of fishes was found by Larrabee (*Proc. Am. Acad. Arts and Sciences,* xlii, No. 12) not to be inherited.

FRANK E. LUTZ.

NOTES AND LITERATURE

ICHTHYOLOGY

Ichthyological Notes.—One of the most valuable papers on the habits of fishes is a study in sexual selection by Cora D. Reeves, "On the Breeding Habits of the Rainbow Darter (*Etheostoma cæruleum*)."[1]

Miss Reeves, a graduate student of Professor Reighard in the University of Michigan, has carefully watched the breeding habits of this dwarf perch, a species in which the males are most brilliantly marked with blue and scarlet.

It appears that the females do not select the brilliant males, that the oldest and strongest males are most brilliant, that the males know the females only by their color, that they mistake young uncolored males for females, and that the bright-colored males frighten away the younger ones by the display of their gaudy fins and by blows of the tail or head. The brilliant males were sucessful in pairing in 60 per cent. of the observed cases. The sexes as usual in vertebrates are equal in number, and the blue and scarlet colors belong to the males alone, these being most brilliant at the beginning of the season—about April first.

These observations give no support to the theory that the females choose the gaudy males. It appears however that the most brilliant males are the oldest and strongest, and that they leave most descendants. This form of the theory of sexual selection would seem to be applicable to bright-colored fishes generally.

MR. E. W. GUDGER[2] shows that the hammer-head shark (*Sphyma zygæna*) feeds on sting-rays and that the mouth and body of the shark are often full of broken-off stings, 50 of these being extracted from a single shark 12½ feet in length from Beaufort harbor.

MR. HERBERT W. RAND[3] discusses the functions of the spiracle of the skate, one of these besides the usual function of respiration is to keep the eyes clean by a jet of water.

[1] *Biological Bulletin,* XIV, 1907.

[2] *Science,* XXV, p. 1005.

[3] AMER. NAT., XLI, p. 288.

MR. CHARLES R. STOCKARD[4] describes the development of the eggs of the killifish (*Fundulus heteroclitus*) in a solution of magnesium chloride.

In this fluid the young fishes develop as one-eyed monsters, the two eyes coalescing into a single median eye. This eye has a single lens. A mixture of sea-water with this solution gives the same effect. The influence of the magnesium salt is therefore supposed to cause the strange development of the eyes.

IN the *Proceedings* of the U. S. Nat. Mus., XXXIII, Jordan and Herre describe the cirrhitoid fishes of Japan, describing one new genus, Isobuna.

IN the same proceedings, Jordan and Richardson describe a new killifish, *Lucania browni,* from a hot spring in Lower California.

IN the same proceedings, Eigenmann & Cole record the species of South American Characin fishes in the National Museum and in the Museum of Indiana University, with numerous plates and descriptions of new species.

IN the same proceedings Professor Edwin Linton describes the worms parasitic on fishes of Bermuda.

IN Bureau of Fisheries Document No. 627, Mr. F. M. Chamberlain records his observations on the salmon and trout of Alaska.

Among other matters of interest it is noted that a majority of the young red salmon spend their first winter in the lakes, while the other species leave early for the sea. It is long known that the red salmon never enter a stream that has not a lake in its course and that they always spawn in streams above a lake. The other four species of Alaska salmon have no special relation to lakes.

Mr. Chamberlain's observations do not confirm the "homing theory." Marked salmon fry from the Naha River appeared as adults at Yes Bay. Most of the fishes however seem to return to the parent stream, from which they probably never wander very far.

Four years is shown to be the usual age of maturity of king salmon and red salmon, while the humpback is probably adult at an earlier period.

[4] *Archiv Entwicklungs Mech.,* XXIII, p. 249.

Mr. Chamberlain's paper contains many valuable facts in relation to the life of salmon, the fruit of nearly four years observation in southern Alaska.

In the *Proceedings* of the Biological Society of Washington (XX, 1907) Evermann and Goldsborough give a check list of the fresh-water fishes of Canada. 145 species are recorded, with a complete list of localities.

In the *Proceedings* of the same society (XXI, 1908), Dr. Evermann describes two new fishes (*Fundulus meeki* and *Salmo nelsoni*) from streams in lower California. The last-named, an isolated troutlet from Mount San Pedro Martir, is especially interesting as occurring farther to the southward than any other known trout. It is apparently an offshoot of the rainbow trout of California, *Salmo irideus.*

In the same *Proceedings* (XXI, 1908) Jordan and Grinnell describe another isolated dwarf waif among the trouts, as *Salmo evermanni.* This troutlet occurs on the headwaters of the Santa Ana River, on Mt. San Gorgonio, in San Bernardino Co., California. It is shut off from the parent form, *Salmo irideus,* by a waterfall, and in isolation it has undergone considerable change. Its origin is parallel with that of the three species of golden trout of the high Sierras. *Salmo evermanni,* living on gray granite, is dull in color with none of the scarlet shades of the golden trout.

In the same connection Jordan and Snyder describe and figure the great Kamloops trout from Lake Kootenay in British Columbia. The specimen figured, sent by John P. Babcock, Fish Commissioner of British Columbia, weighed 22 pounds. This species is an offshoot of the steelhead trout, *Salmo rivularis.*

In the *Bulletin* of the Bureau of Fisheries, XXV, for 1906 (October 25, 1907), Jordan and Snyder record a number of new species from Hawaii, with several plates, four of them in color. The new species are *Caraux dasson, Ariommus evermanni, Rooseveltia aloha, Thalassoma neanis* and *Scaridea aërosa.*

The advent of Japanese fishermen in Hawaii has caused many very rare deep-water fishes to be common in the markets; among these is the type species, *Rooseveltia brighami,* of the genus named for the naturalist Theodore Roosevelt. This species, scarlet and gold, is one of the most brilliant in Hawaiian waters.

In the same *Bullein,* Dr. M. X. Sullivan discusses in detail the digestive tract in sharks.

In the same *Bulletin* (Vol. XXVI, 1907), Evermann and Goldsborough give a catalogue of the Fishes of Alaska, with many plates, based primarily on the collections made by the Albatross in 1903, under the direction of Jordan and Evermann. The following new species are described and figured:

Polistotrema deani	*Blennicoltus clarki*
Sebastodes swifti	*Pholis gilli*
Icelinus burchami	*Lumpenus longirostris*
Coltus chamberlaini	*Lycodes jordani*

Many corrections in synonymy are made. One of these the present writer does not accept. He believes that the two large rays of Monterey Bay, *Raja stellulata* and *Raja rhina,* are both distinct from *Raja binoculata* and from each other. The authors have overlooked *Bryostemma tarsodes* described from Alaska by Jordan and Snyder.

This paper is a most useful one to students of Alaskan fishes.

In the *Journal* of the Imperial Fisheries Bureau of Japan, Dr. K. Kishinouye describes the natural history of the sardine of Japan (*Sardinella melanosticta*) and the related species.

For some unexplained reason, he unites the Pacific herring *Clupea pallasi* with the Atlantic *Clupea harengus.* New species of sardine are described under the names of *Clupea immaculata, Clupea okinawensis* and *Clupea mizun.* These belong to Sardinella, and the last two are from the Riu-Kiu Islands. A new anchovy is described as *Engraulis koreanus.* This should belong to the modern genus Anchovia, being very different from *Engraulis japonicus.*

In the *Journal* of the College of Science, of the Imperial University of Tokyo (XXI, 1907), Professor S. Hatta of Sapporo describes the gastrulation of the embryo of the lamprey.

In the *Proc. Zool. Soc., London* (1906), Professor Bashford Dean has notes on living specimens of the Australian lung-fish (*Neoceratodus forsteri*). Its movements are notably those of an amphibian rather than a fish.

In the *Annals* of the Museum of Natal, Mr. C. Tate Regan describes new species from that coast. A species of remarkable interest is a new saw-shark, *Pliotrema warreni,* with six gill-slits.

In the *Annals* of the Museum of Vienna, XXI, 1906, Dr. Viktor Pietschmann has a valuable record of the fishes collected in a voyage to Iceland, and another to Morocco.

In *Records* of the Australian Museum, VI, 1907, Allan R. McCulloch describes the fishes and crustaceans taken by the Woy Woy, in deep waters of the Tasman Sea. The most notable of the new species is the sculpin-like fish, *Hoplichthys haswelli.*

In the *Journal of the Linnæan Society of London*, Mr. A. D. Darbishire describes the water current in the spiracle of sharks.

In the *Sitzber.* of the same museum, Vienna, Vol. 116, 1907, Dr. Viktor Pietschmann describes new sharks from Japan, *Centrophorus steindachneri* and *Etmopterus frontimaculatus.*

The last species was also taken by Jordan and Snyder in Sagami Bay, in company with *Etmopterus lucifer.* It is one of the smallest of sharks, black, with a milk-white spot on the top of the head.

In the *Proc. Zool. Soc., London* (1907), Mr. Regan redescribes *Velifer hypselopterus,* a Japanese species not seen in the last fifty years, from three specimens in the British Museum. A second species from northern Australia is described as *Velifer multiradiatus.*

In another paper Mr. Regan brings together the aberrant genera Lampris, Velifer, Trachypterus and Lophotes, framing of these a new suborder *Allotriognathi.* These fishes, like the Berycoids have an orbitosphenoid, but no mesocoracoid bone. Mr. Regan thinks that these fishes are derived from the berycoids, and the latter from forms like the extinct *Ctenothrissa* and *Pseudoberyx.* These observations of Mr. Regan are very interesting and his conclusions seem reasonable. He notes that Semiophorus is allied to Platax and not to Lampris.

In "Wissenschaftliche Ergebnisse einer Zoologischen Expedition nach dem Baikal-See" (1907), Dr. Leo Berg discusses the sculpin-like fishes of Lake Baikal, the Cottidæ, Cottocomephoridæ and Comephoridæ. The excellent monograph is preceded by a careful account, fortunately in German not Russian, of the osteology of these fishes. Of the 34 species of fishes found in Lake Baikal 17 are endemic, or developed in the lake, not occurring elsewhere. Of these, two genera, Comephorus and Cottocomephorus, each constitutes a distinct family. Other genera

peculiar to this lake are Abyssocottus, Cottinella, Limnocottus, Procottus, Batrachocottus and Asprocottus. The fauna described in this paper is one of peculiar interest.

In another paper in the *Annuaire de l'Académie de St. Petersbourg,* XI, 1906—unfortunately entirely in Russian—Mr. Berg discusses the Old World species of minnows of the genus Phoxinus.

In the same *Annuaire,* vol. XII, 1907, Mr. Berg treats in Russian and in English, the fresh-water fishes of Corea. The genus Longurio of Jordan and Starks is united by Berg to Saurogobio of Bleeker, and Fusania with Aphyocypris of Günther. In another paper Mr. Berg discusses Siberian species of Rhodeus.

In the "Fauna America-Centrali" Mr. C. T. Regan continues his account of the fishes of Mexico and Central America. *Amiurus meeki* is described from Chihuahua, *Moxostoma mascotæ* from Jalisco, *Algansea affinis* from Rio Lerma, *Algansea stigmatura* from Rio Grande de Santiago. Several species recognized by other authors are placed in synonymy. In some cases this process exchanges one doubtful opinion for another.

In *Popular Science Monthly,* LXXI, January, 1908, Dr. Jordan describes "The Grayling at Caribou Crossing," a running descriptive account of the Yukon country, with a dash of angling.

In *Science,* XXVI, 1907, Dr. Bashford Dean reviews Dr. Eastman's recent papers on the "Kinship of the Arthrodires," Dr. Eastman claims that these mailed fishes are Dipnoans and to this conclusion Dr. Dean enters a "friendly protest."

In the *American Journal of Anatomy,* VII, 1907, Dr. Dean discusses the structure and origin of the Acanthodian sharks, one of the most primitive of the extinct forms. Their relationships are with Cladoselache, a form having fins of the fin-fold type, and probably the most primitive of known sharks.

In *Archives de Zoologie Experimentale,* VII, 1907, Dr. Louis Fage describes the fishes of the Balearic Islands, with several new species. The paper can be especially praised for its attention to laws of nomenclature, as also for the accuracy and fullness of its accounts of the new forms. Two species are referred to the genus Eleotris, a group not hitherto recorded from Europe. Neither of the species, however, belongs to Eleotris

proper. *Eleotris pruvoti* is an ally of Valenciennea and *Eleotris balearica* approaches Gymneleotris.

Dr. Jacques Pellegrin publishes in the "Mission Scientifique," 1907, an account of the fishes of the high mountain lakes of South America.

In a weekly Journal, the *Sydney Mail*, Mr. Charles Thackeray gives a readable and accurate account of the game fishes of New South Wales, with wood cuts of the leading species.

ECHINODERMATA

The Stalked Crinoids of the Siboga Expedition.[1]—There has recently been published a monograph on the recent stalked crinoids of the East Indies, based on collections made by the *Siboga* which is the first important contribution to our knowledge of the group since the publication of Dr. P. Herbert Carpenter's great work (the *Challenger* report) in 1884.

The first thing to attract the attention of the student of the recent crinoids is the announcement of the discovery of the infrabasals in a species of Metacrinus, *M. acutus*, a new species here first described. Dr. Carpenter stoutly maintained that infrabasals did not occur in any species of recent crinoid, and he criticized rather sharply the so-called law of Wachsmuth and Springer, by the application of which the recent genera Isocrinus and Metacrinus were shown to be dicyclic. He dissected numerous specimens of various species of both genera, and according to his statements and figures, appeared to conclusively prove their absence. In 1894 the Swiss paleontologist de Loriol discovered and figured infrabasals in a fossil species of Isocrinus, and now Professor Döderlein shows their presence in Metacrinus. This discovery by Dr. Döderlein was made simultaneously by the present reviewer in two other species of Metacrinus and in *Isocrinus decorus* and announced in a paper now in press, which had gone through the final proof before Dr. Döderlein's contribution was received. In this the infrabasals of *Metacrinus rotundus* from Japan and of *M. superbus* from the China Sea, and of *Isocrinus decorus* from Cuba are described and figured.

[1] Die Gestielten Crinoiden der | Siboga-expedition | von | L. Döderlein. | Monographie XLIIa aus | Uitkomsten op Zoologisch, | Botanisch, Oceanographisch en Geologisch gebied | verzameld in Nederlandsch Oost-Indië 1899–1900 | aan boord H. M. Siboga onder commando van | Luitenant ter zee 1e Kl. G. F. Tydeman | uitgegeven door | Dr. Max Weber.

The *Siboga* dredged stalked crinoids at seventeen stations, in all more than sixty specimens representing thirteen species and two additional varieties. Three of these species are referred to Bathycrinus, one to Rhizocrinus, two to Isocrinus, and the remainder to Metacrinus, while the species of Rhizocrinus dredged by the *Valdivia* off Somaliland and recorded by Chun in 1900 is included in the report, and figured under the name of *R. chuni.*

The species referred to the first two genera are of very exceptional interest, apart from the fact that neither genus has been recorded from the East Indian region; while the Rhizocrinus (*R. weberi* n. sp.) is related to *R. rawsonii* of the tropical Atlantic, the three Bathycrinus are in their characters quite unlike anything previously known; in the first place, they are all very small, one species, *B. poculum,* being only 8 mm. in total length, while none of the others exceeds 35 mm.; but, most remarkable of all, they unite the characters of Bathycrinus and Rhizocrinus so completely as to leave scarcely any grounds for considering them as distinct genera. This discovery was not news to the present reviewer; for the day after the receipt of Dr. Döderlein's work, his own description of two intermediate species, *Bathycrinus equatorialis* and *B. caribbeus* was published. Rhizocrinus (including, as we now apparently must, Bathycrinus) contains at the present writing fifteen described species, *of which nine have been made known during the past year, and there are several additional species now in press;* it is very evident that our knowledge of even this comparatively old genus is still extremely rudimentary. Dr. Döderlein's interesting remarks on the shedding of the arms in Rhizocrinus—Bathycrinus I shall consider in detail later.

Isocrinus naresianus, first found by the *Challenger,* was rediscovered by the *Siboga* off the northern end of Celebes, having been previously known only from the Kermadec and the Meangis Islands, and from Fiji, and a new species, *I. sibogæ,* was discovered near Timor. This last belongs to the group of the genus in which the costals and division series consist of two joints, bound by syzygy, including such species as *I. wyville-thomsoni, I. parræ* (of Guérin 1835 = *I. mülleri* of Oersted 1856 of which *I. maclearanus* is merely a variety) and *I. alternicirrus,* to the last of which *I. sibogæ* is most nearly related, though it possesses the normal arrangement of the cirri. The form *maclearanus,* by the way, did not come from the southwest Atlantic as stated by

Dr. Döderlein, but from the west central Atlantic; moreover, it was first described by Wyville Thomson, and not by Carpenter; also *I. wyville-thomsoni* was first described by Wyville-Thomson, Jeffries's mention of the name being in both cases a pure *nomen nudum.*

The discussion of Metacrinus is appropriately begun with an account of the infrabasals of *M. acutus,* which are compared to those of *Millericrinus polydactylus.* Then follow paragraphs on the specific characters of the genus found in the calyx, the arms, and the stem, which last is believed to furnish the most reliable characters. In this conclusion I heartily concur. The stems are considered at some length, and there is an interesting account of the stem growth, a subject which I shall discuss at some length later. Dr. Döderlein believes that, when living on the sea-bottom, the species of Metacrinus have very long stems, which are inextricably entangled one with another, forming a sort of mesh-work, from which the younger part of the stem and the crowns stand out; in other words, that the individuals form a sort of crinoid colony, the crowns arising from a maze of stems, and he adduces considerable strong evidence in support of this view. It will interest him to know that I have additional evidence pointing to the same conclusion.

The species of Metacrinus obtained by the *Siboga* all fall into that division of the genus in which there are "five radials," two of which are united by syzygy; three new species, *M. acutus, M. serratus* and *M. suluensis,* and a new variety, *M. nobilis timorensis,* are described, while that somewhat unhappy word *typica* is used to denote the typical forms of *M. nobilis* and *M. superbus. M. acutus* comes from the Ki Islands, and *M. serratus* and *M. suluensis* were found in the Sulu Archipelago. *M. nobilis timorensis,* as its name indicates, occurs near Timor. *M. cingulatus,* previously known from the Ki Islands and the Arafura Sea, was rediscovered at the Ki Islands and at Timor; *M. varians,* from the Kermadec and Meangis Islands, was found at Timor, the Ki Islands, and in the Sulu Archipelago; and a varietal (unnamed) form of *M. superbus* was collected at the Ki Islands. *Metacrinus nobilis* is divided into three varieties, *typica, murrayi* and *timorensis,* with somewhat unfortunate nomenclatorial results; for the specific name *murrayi* of Carpenter has precedence over *nobilis* of the same author. Expressing these names as trinomials, we have *Metacrinus mur-*

rayi murrayi, M. murrayi typica, and *M. murrayi timorensis,* the *typica* not representing the typical form at all. *Metacrinus murrayi* (to speak with nomenclatorial accuracy), previously known from the Ki Islands and Arafura Sea, was again found at the Ki Islands, and also at Timor.

Perhaps it is wisest to do as Dr. Döderlein has done and recognize by name the various geographical variations of the Metacrinus species, but it certainly conjures up a terrible vista of possibilities, for it is difficult to imagine more variable organisms than the species of this genus, according to my experience. I have examined some additional varieties of *M. superbus* from Japan, and a bewildering, though small, series of *M. angulatus* from the same locality, some of which fall into the group with "five radials," and others into that with eight to twelve, while *M. rotundus,* also falling into both groups, is even more variable; and it seems to me that if we once get a good start on the trinomial system in any branch of the recent crinoidea, with the continuance of the present activity in the field, it will not be long before each genus will require a specialist for its elucidation.

Dr. Döderlein is to be congratulated on the results of his study of the *Siboga* collection, and the production of a volume which will long stand as the authoritative work on the stalked crinoids of the East Indian seas, and which not only treats of the stalked crinoids systematically as a class, but suggests many interesting new lines of investigation, and bears throughout the stamp of one who not only has an exhaustive knowledge of the group under consideration, but of many different forms of animal life as well.

AUSTIN HOBART CLARK.

U. S. BUREAU OF FISHERIES.[2]

ANIMAL PATHOLOGY

Trypanosome Diseases.—Recent investigations which have been carried out in foreign laboratories with the object of ascertaining the mode of cure for sleeping sickness, and other trypanosome diseases have resulted in demonstrating certain features in the biological conduct of these protozoa towards chemical stimuli which are of extreme interest. Thus far only three

[2] Published with the permission of the Commissioner of Fish and Fisheries.

groups of chemicals have been discovered which are efficient in the treatment of trypanosome infections. They are: (*a*) benzidin dyes, (*b*) basic triphenyl-methane dyes and (*c*) arsenical compounds. In experimental animals complete cure has apparently been effected by maximum doses of these compounds. With lesser doses and prolonged treatment the parasites may disappear from the blood for a time, but later on make their appearance again. Those which recur have undergone a pronounced change in their biological characters and constitute a strain resistant to the therapeutic agent employed. Such a strain manifests chemoresistance of a specific character towards the particular substance used to develop it and an increased resistance towards other compounds of the same group. On the other hand, the development of resistance towards one group causes no increase whatever in the resistance towards other groups. By continued experiments, however, a strain has been produced manifesting a triple resistance, specific towards each of substances employed.

Chemo-resistance, once acquired, persists unchanged while the resistant trypanosomes are passed through normal animals even for one hundred and forty transfers extending over fourteen months. This has been cited as strong evidence of the transmission of acquired characters. The specificity of the resistance is very striking. After an experimental animal has been inoculated with a mixture of two resistant strains and is then treated with a substance towards which one of the elements is resistant, the other element will disappear from the blood, but the resistant strain will remain and develop unchecked. Indeed, the two strains remain separate and capable of isolation after repeated passages through infected animals. Or, in other words, a strain with double resistance or with modified resistance does not arise as the result of infection with a mixture of two resistant strains.

Henry B. Ward.

ANIMAL BEHAVIOR

Recent Work on the Behavior of Higher Animals.—There exist to-day two main centers for the strictly scientific and experimental study of the behavior of the higher animals. One is at Harvard, led by Yerkes, the other at Chicago, under Watson. Excellent work appears at times from other quarters, but it can usually be traced to the influence of one of the two men named. There is a third independent center for such work at Clark

University, but lacking the single-minded leadership of the other two, the attack on the problems has there been less unified and effective. Thorndike, whose work some years ago gave such impetus to the whole subject, has unfortunately been drawn into other work, or we should doubtless have another most effective center for such investigations. Outside of the United States the scientific study of the behavior of the higher animals is a negligible quantity, compared with what comes from the centers named. The active French movement in comparative psychology, under the influence of Bohn, Piéron and others, has been thus far limited mainly to the invertebrates.

At the laboratories we have named the work on animals is carried on by the aid of such accurate appliances and methods as have long been developed for the investigation of the physiological psychology of man, with ingenious modifications and additions as required by the peculiarities of the subject. This gives the work an almost uniquely precise and scientific character, as compared with most other studies in animal behavior. Most other workers have been compelled to content themselves with apparatus, observations and experiments of a more "homemade" character. The two leaders, one by training a zoologist and psychologist, the other a physiologist and psychologist, have been devoting themselves largely to rats and mice of late, while followers have made side excursions into the territory of cats, dogs and raccoons. It is necessary to concentrate the attack somewhere, and for the present the rats and mice are bearing the brunt. We shall pass in review the recent contributions from the centers named, limiting ourselves at present to work influenced from Harvard.

From Harvard we have first the elaborate study of the dancing mouse, by Dr. Yerkes.[1] Perhaps the most striking feature of this work lies in the elegant and fertile methods devised by the author, and of course in the results attained by these methods. The main method consists in a sort of "Lady or the Tiger" alternative presented to the unsuspecting mouse. He is invited to enter one of two doors; one leads to an electric shock, the other to freedom and food. The fateful portals are marked with signs of various sorts,—cards of different shapes, markings, color, brightness, odor, etc. The "right" and "wrong" doors can be alternated at the will of the experimenter, as can

[1] Yerkes, R. M. The Dancing Mouse, a Study in Animal Behavior. The Animal Behavior Series, Vol. I, 290 pages. The Macmillan Co., 1907.

the signs. The mouse in repeated experiments tries at first the simple plan of returning to the right or left door according as he has found that to be correct. When he finds that the correct portal is being alternated, he quickly learns to alternate in his choices. But when he finds that there is no regularity in the alternations, he begins to pay careful attention to the signs posted about the portal; "to run from one to the other, poking its head into each and peering about cautiously, touching the cardboards at the entrances, apparently smelling of them, and in every way attempting to determine which box could be entered safely." Often the mouse runs from one portal to the other twenty times or more, before deciding which to enter. Now, it is in this state of uncertainty and concern that the mouse is ready to give interesting results in animal education and in sense physiology. He uses all his senses to the best of his ability in determining which is the "right" door to enter, so there is opportunity, which Dr. Yerkes has skilfully used, to test his senses, and at the same time to study his ability to learn. When the two portals are indicated, the "right" one by a light card, the "wrong" one by a dark card, the mouse learns to choose the correct card. If for both cards are substituted others that are of deeper shade, but have a similar relative brightness, the mouse continues to choose the one of lighter shade. He has learned, not that a particular card, or a particular shade, is the right one, but that the *lighter of the two* is the one to choose; he often runs back and forth many times, seeming to compare them carefully. By accurately grading the difference in brightness between the two portals, it was possible to determine just what differences the mice could discriminate, giving an opportunity for work on Weber's law. *The mice rapidly learned to discriminate finer and finer shades of difference.* A certain mouse, in a first series of experiments, could discriminate only when the difference in brightness was practically half the greater brightness. In a later series he could discriminate when the difference was but one fifth and, after much more practise, when the difference was only one tenth. Such educability at first carried confusion into the data designed to test Weber's law. When it was finally taken into account, the law was found to hold.

In a similar way Yerkes made extensive studies of color vision in the mouse. He found that apparently they do not see colors,

at least not as we do; that most of their apparent discrimination of color is due to differences in brightness; and that the brightness of different colors is not the same for them as for ourselves.

It is extraordinary that the mice were unable to discriminate the portals by different shapes of cards or of lights. They showed no power of distinguishing forms.

We have given some samples of Yerkes' methods and results; many other matters of equal or greater interest were studied, by varied methods, including the classic one of using labyrinths. The author's experiences are set forth in interesting chapters on educability, methods of learning, the efficiency of different methods of training, the duration of habits, the revival of lost habits, individual differences in behavior, and the like. When it comes to responding to experimentation, the dancing mouse is, as its name indicates, rather an artistic than a strictly utilitarian animal, giving a delightful variation from those orthodox creatures whose main desire is to "get there," so that results are not readily expressed correctly in terms of minutes required and space passed over. "Most mammals which have been experimentally studied have proved their eagerness and ability to learn the shortest, quickest, and simplest route to food without the additional spur of punishment for wandering. With the dancer it is different. It is content to be moving; whether the movement carries it directly to the food-box is of secondary importance. On its way to the food-box, no matter whether the box be slightly or strikingly different from its companion box, the dancer may go by way of the wrong box, may take a few turns, cut some figure-eights, or even spin like a top for a few seconds almost within vibrissa-reach of the food-box, and all this even though it be very hungry."

In addition to the strictly experimental work, Yerkes gives a full account of the peculiar "dancing" movements that have given the animal its name; a sketch of what we know of its history, and an extensive discussion of the disputed question as to whether its ears are defective and whether it is deaf. Yerkes concludes that it can hear only for a few days, when about two weeks old.

Altogether, Dr. Yerkes' book is one of the most attractive as well as one of the most valuable of the strictly scientific studies of animal behavior. It would be venturing out of the

"strictly scientific," but one wishes that the author might give us an imaginative picture of what life and the universe may be in the consciousness of this little creature, that does not hear, sees little or nothing of colors, can't distinguish a square box from a round one nor a circular card from a triangular one, feels impelled to "cut figure eights and spin like a top" on its way to a dish of food, and learns many things rapidly and well. Possibly such an unscientific picture could be appended to the really scientific account without injury to the latter! Dr. Yerkes is still studying the dancing mouse, and may some time feel prepared to give us such a picture.

Or perhaps we must look for such pictures to the second volume of the Animal Behavior Series, of which this is the first! The second one, just announced, is a volume on "The Animal Mind," by Margaret Washburn. The Series, edited by Dr. Yerkes, promises to be of the greatest value.

A matter that has been most in need of study is the part played by imitation in the behavior of higher animals. Years ago imitation was the favorite refuge of those who wished to explain the remarkable actions of animals without attributing to them higher intellectual powers. When Tabby pressed the latch and walked out the door, that was because she had seen some one do it. Then came Thorndike, and changed all that. To give imitation in place of reason as an explanation, says Thorndike, is to substitute one false explanation for another. In studying cats and monkeys, Thorndike saw no signs of imitation either of one another or of man. And most later investigators have agreed that imitation plays little part in the behavior of animals, at least in comparison with what had been supposed. Even the monkey, we are told, rarely imitates man or other monkeys. Direct, unreflective imitation of simple sounds or movements—the performance of an act merely because a companion has performed it, without reference to results—is less rare, though likewise not so common, as had been supposed. But the imitation of an act because that act accomplished a certain result, and in order to accomplish the same result—this was not found, though this is the kind of imitation assumed in current explanations to be common. The extensive experiments of Hobhouse,[2] evidently undertaken with the expectation of finding imitation playing a part, are striking as an example of how

[2] Mind in Evolution, Chapter VIII.

little it is possible to find, and how uncertain is what is found, even with the best of will. Kinnaman, Small and others had incidentally seen a few examples of real imitation. We have now from the Harvard laboratory two careful studies of this matter by Berry,[3] with results that are most interesting. In Berry's rats and cats we find imitation as it were in the making. Our conception of imitation, and of its different kinds, loses its sharp lines and angles and becomes indefinite. When one knows how to escape or get food and another does not, the animals do not set to work to imitate each other's actions in the clear-cut way we are apt to think of as imitation. But the one that doesn't "know how" does after some time begin to pay attention to his comrade's actions, and then in an indefinite way to do something of the same sort himself. "We found that when two rats were put into the box together, one rat being trained to get out of the box, and the other untrained, at first they were indifferent to each other's presence, but as the untrained rat observed that the other was able to get out, while he was not, a gradual change took place. The untrained rat began to watch the other's movements closely; he followed him all about the cage, standing up on his hind legs beside him at the string, and pulling it after he had pulled it, etc. We also saw that when he was put back the immediate vicinity of the loop was the point of greatest interest for him, and that he tried to get out by working at the spot where he had seen the trained rat try."[4] In cats similar and more marked cases of imitation were found and analyzed.

Berry's work is the first really scientific study of imitation in animals that we have had, and it shows, as so commonly happens when a thorough study is made, that we can not make extreme statements, whether positive or negative. Imitation is found; even "reflective imitation," but it is not precise; we can often hardly be certain whether it *is* imitation; and where it is more pronounced it is difficult to distinguish imitation for the mere sake of doing what a companion does, from imitation for the purpose of accomplishing the result that the companion accomplishes. Like all other traits of behavior, imitation grows gradually out of something that seems not the same thing at

[3] Berry, C. S. The Imitative Tendency of White Rats. *Journ. Comp. Neurol. and Psychol.*, 16, 333–361. *Id.*, An Experimental Study of Imitation in Cats. *Ibid.*, 18, 1908, pp. 1–25.

[4] Berry, The Imitative Tendency of White Rats, p. 358.

all! Whether to call this "something" by the same name as the developed activity is one of the frequent grounds for unprofitable controversy.

L. W. Cole[5] has made an elaborate investigation of the intelligence of raccoons, with results of more than usual interest. The raccoons are compared throughout with the famous cats of Thorndike, and the work, like most recent work on animal intelligence, follows the outlines of the well known paper of the author just mentioned.[6] But Cole has made real and important advances in both method and results. The raccoons are either much more clever than the cats, or the methods employed were better fitted for bringing out latent possibilities; probably both these things are true. The experiments consisted largely in allowing the animals to learn to open boxes closed by fastenings of various degrees of complication. The raccoons learned somewhat more readily than the cats. As in all other animals, their learning was largely by trial and error. But they are not restricted exclusively to that method, as Thorndike maintained to be the case for the cats; decidedly not if we limit that method to the *gradual* formation of an association between a motor impulse and a sense perception. (1) There was clear evidence that the animal at times, catches the idea, that a certain act is what opens the door, so that he later acts directly and at once on that idea. It is not a mere gradual exclusion of useless movements, till only the useful ones are left. (2) The raccoon learns by being put through an act. It learns without "innervating its muscles," the great test for the possibility of learning in Thorndike's cats. It learns to go into a box by a certain entrance, through having been *lifted* into the box that way a number of times. By being put through them, it learns certain acts which it was unable to learn by its own efforts. By putting different raccoons through the same act in different ways, they learned to perform it in different ways; for example, one learned to lift a latch with its paws, another with its nose. (3) While the raccoons, like most other animals, do not imitate each other or any one else in a marked degree, they did, after seeing the experimenter perform a certain action many times, "catch the idea" and endeavor to perform the action for themselves. This

[5] Cole, L. W. Concerning the Intelligence of Raccoons. *Journ. Comp. Neurol. and Psychol.*, 17, 1907, pp. 211–261.

[6] Thorndike, E. L. Animal Intelligence. *Psychol. Review*, Monograph Suppl., vol. 2, 1898.

is of course the essence of "reflective" imitation. (4) Thorndike concluded that cats have probably no "free ideas"; no stock of images which are motives for acts. The association in the cats was always between a motor impulse and a present sense perception; there was no association *of ideas.* This negative conclusion was based largely on the inability of the animals to learn from being put through an act. In this latter matter, Cole calls the reader's attention particularly to *"the radical difference at every point"* between the cats of Thornidike's experiments and the raccoons of his own. "If inability thus to learn is evidence against the presence of ideas, then ability to do so should be equally strong evidence for it." Furthermore, Cole gives much additional evidence for the presence of ideas in the raccoons; and certain results of some extremely ingenious experiments amount to a demonstration that the animals do hold mental images, so far as such a thing can be demonstrated.[7] The animals seemed to remember definite objects for a time, then forget them; then suddenly, under certain conditions, recall them. They fought against being put into boxes with complex fastenings, from which they had some time before had difficulty in escaping, though they willingly went into similar boxes whose fastenings they had found simple. In certain experiments there were two alternative signs to be raised; the green one meant food, the red one meant none. The raccoons learned to raise these signs by clawing at the standards, but they could not see beforehand which sign would come up by clawing at a certain standard. *When the red one came up they clawed it down again,* then clawed up the green one, and made ready to receive food. Clearly, the red sign did not correspond to an image that the animal had in mind, while the green one did. Other experiments were devised in which success depended on the animal's holding in mind the images of certain things that had gone before; the raccoons stood these tests successfully. It is difficult to see how there could be more conclusive proof of the presence of ideas in animals that can not talk.

[7] A subjective thing, such as an idea, can, of course, not be absolutely demonstrated by objective methods. It is always possible to substitute for the idea its physiological accompaniment, and say that this is all that we can be assured of. In other words, "demonstration of the existence of ideas" in animals can never go further than to show that *they act as men do when men have ideas.*

The interesting paper of Hamilton[8] is perhaps in its origin independent of the Harvard laboratory. We have seen that the dancing mouse learns to act on the basis of a comparison between two things, selecting, not a particular thing, but the lighter of two, or the darker of two, etc. Kinnaman found that the monkey could similarly learn to choose always the lighter vessel, or to choose the colored vessel from among a number of vessels, even when the colors were changed. Hamilton made a precise study of a similar sort of action in a dog. The animal learned that in order to escape from a pen and get food he must press, out of a number of levers, the one that bore the same sign that was found on a general sign-board elsewhere in the pen. In successful cases his method of procedure was, then, to inspect the general signboard, then to pass in review the four levers till he found the one that bore the same sign—then to press this. This appears to involve a fairly complex mental operation (if we may venture to interpret the actions of animals from that highly reprehensible standpoint). The dog clearly learned to choose in the way described. But unfortunately, being a clever dog, he after a time discovered a much simpler method of action that accomplished the same results. He merely began at one end of the series and pressed the levers in order till he came to the one that worked. When electric shocks were attached to the "wrong" levers, he decided that he didn't care to play at that game any longer, and the experiments had to end.

How far such action, seeming to involve complex mental operations, may be demonstrated in animals when there has been fifty years' development of method and results in such investigations, instead of merely two or three attempts at it, is a question that deserves consideration by those who are so ready to deny, on the basis of what we now know (or rather, on the basis of what we don't know), all mental complexity in animals.

Indeed, it is clear that much of the work we have just reviewed consists in showing experimentally that the mental operations of animals are more complex than had been supposed; in restoring to animals certain things that had been denied them. And this is typical. The recent history of the study of animal

[8] Hamilton, G. van T. An Experimental Study of an Unusual Type of Reaction in a Dog. *Journ. Comp. Neurol. and Psychol.*, 17, 1907, pp. 329–341.

behavior has shown a curious parallelism in each of its three great divisions. In each division the slate was, as it were, wiped clean some ten or fifteen years ago; the existing structure was razed to the ground, and we have been building it up again ever since. In the lower organisms Loeb reduced the phenomena to almost inorganic simplicity. For the ants, bees and other higher invertebrates Bethe took similar action; they were stripped of their fanciful decorations of memory, intelligence, etc., and left absolutely devoid of "psychic qualities" of any sort; their behavior was composed of invariable reflexes and tropisms of the simplest character. Thorndike performed the same operation for the vertebrates. Not only did they not reason (preposterous notion!), but they did not imitate, could not learn by seeing a thing done nor by being put through an act, nor by any other way than by simply gradually dropping out useless movements from among those made at random; and they had not even *ideas* of things past, to say nothing of perceiving relations or being capable of trains of thought or of formulating a plan.

In all three divisions of the subject the work since these operations has consisted largely in the slow and painful restoration, by precise experimental methods, of what was thus wiped out at one fell swoop. The three authors named, with those that aided them, perhaps did the science of behavior the greatest possible service at that time. Before them there was hardly an ordered science in this subject; there was a jungle of suppositions, assumptions and anecdotes. Loeb, Bethe, Thorndike and Company destroyed all this and compelled us to rebuild from the ground up, a solid structure, based on precise scientific methods. How high the structure will have to go, no one can foretell; certainly it is not yet finished. Indeed, animal behavior as a science is merely in its swaddling clothes; it can not carry as yet many sweeping conclusions, particularly negative ones. General negations based on what we now know are most unscientific; they are largely capitalizations of our large stock of ignorance. It behooves the man of science, therefore, to be careful in his destructive criticisms; some recent controversies show that this caution is much needed. It will be long before our science is coextensive with the phenomena with which it is attempting to deal. H. S. Jennings.

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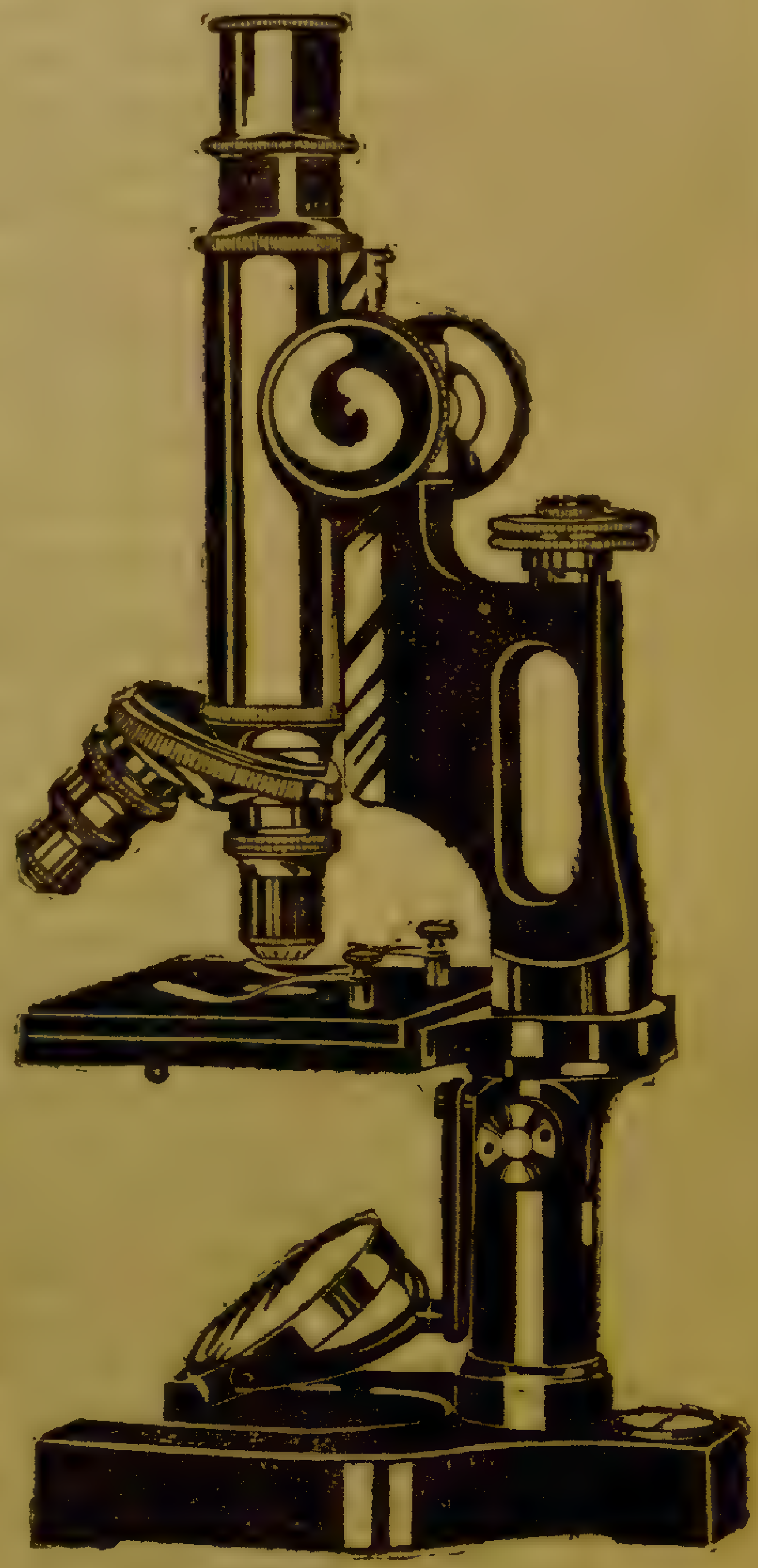

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Boston Society of Natural History,
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GLOVER M. ALLEN, *Secretary*

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DEVOTED TO THE NATURAL SCIENCES
IN THEIR WIDEST SENSE

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ASPECTS OF THE SPECIES QUESTION

At the recent Chicago meeting of the Botanical Society of America, the afternoon of Wednesday, January 1, was devoted to a symposium on "Aspects of the Species Question." The principal participants, who, upon invitation of the council, prepared and read papers at the symposium, were: C. E. Bessey and N. L. Britton, who discussed the taxonomic aspect; J. C. Arthur and D. T. MacDougal, who spoke on the physiologic aspect; F. E. Clements and H. C. Cowles, who dealt with the ecologic aspect of the question. The reading of the papers was followed by an open discussion of the question by a number of the members present. The papers read and the corrected stenographic report of the discussion are printed below.

D. S. JOHNSON,
Secretary.

OFFICE OF THE SECRETARY,
BALTIMORE, MD., March 1, 1908.

THE TAXONOMIC ASPECT OF THE SPECIES QUESTION

PROFESSOR CHARLES E. BESSEY

THE UNIVERSITY OF NEBRASKA

As long as species were supposed to be actual things, "created as separate kinds at the beginning," that botanists "discovered," as explorers discover islands in the ocean, there was no serious "species question." A botanist might make a mistake, and announce the discovery of a new species, when he had merely found a variety of an old species; as an explorer might mistakenly announce the discovery of a new island, when as a matter of fact he had only seen an unfamiliar coast of a long-known island.

Nature produces individuals, and nothing more. She produces them in such countless numbers that we are compelled to sort them into kinds in order that we may be able to carry them in our minds. This sorting is classification—taxonomy. But right here we are in danger of misunderstanding the matter. We do not actually sort out our individuals. We imagine them sorted out. It is only to a very slight extent that the systematic botanist ever actually sorts out individuals. When he has a considerable number of individual dried plants in his herbarium, he may sort them out, but these are but an infinitesimal portion of all the individuals in the world that we imagine to be sorted, but that are actually unsorted.

So species have no actual existence in nature. They are mental concepts, and nothing more. They are conceived in order to save ourselves the labor of thinking in terms of individuals, and they must be so framed that they do save us labor. If they do not, they fail of

their purpose. Here we perceive one of the principles which must control in the limitation of species. If we multiply our species unduly we approach too near to the individuals, and we are as much burdened as though we had not invented species. On the other hand, if we make too few species those we do make include so many variations from the type that confusion results again. We must steer a course between these two extremes.

I am well aware that every man who has split up species upon any pretext will at once lay his hand upon his heart and assure himself that he has done this very thing of avoiding these extremes. I have yet to find a man who has not felt that all of his species were conservatively made, and that had he been radically inclined he could have made many more. And yet the fact remains that much of the species-making of recent years has rendered it vastly more difficult than formerly for us to obtain a grasp of the flora of a region. Instead of helping us, this perverted notion of the purpose and the proper limitation of species has actually proved to be a hindrance. How much, for example, does the average botanist know nowadays about the species of Cratægus? It will not avail to say that "he knows as much as he ever did," for once he did study them somewhat, but now he is compelled to pass them by as quite too difficult for him to undertake to distinguish with the time he has at his command. The inordinate multiplication of species has hindered instead of advanced our knowledge, and this fact is sufficient to condemn it utterly.

We are in danger of destroying the usefulness of taxonomy in our zeal for describing every differing form as a separate species. We have lost sight of the primitive reason for the formation of species, namely, that we should have fewer things to hold in mind. Primitively the aim was to have as few species as possible. Now too often we look upon the addition of new species as a contribution to knowledge, when, on the contrary, it may be a hindrance.

The Linnean conception of species may have been too broad, but it had the merit of being understood. It has yet to be shown that that conception of species has been outgrown. The human mind is pretty nearly the same to-day that it was a century and a half ago. The botanists of to-day may be able to recognize species where Linné, and DeCandolle, and Gray could not, but the difference is by no means great enough to warrant such great changes as have taken place in the conception of species by some recent systematists. The human mouth is probably a little smaller than it was thousands of years ago, and probably the tendency is to a reduction of its dimensions, but it certainly has not changed so much as to warrant a marked reduction in the size of tablespoons; much less does it give sanction to any proposal to reduce them to the size of miniature saltspoons! The old spoons that still fit the average human mouth very well are not likely to be displaced for much smaller ones. I think it is highly probable that in like manner we shall insist upon the old measure of species, for the good reason that it is still well fitted to our mental needs and mental capacity. The experience of botanists as a body sanctions the general idea and limitations of species as understood by Linné, by DeCandolle, by Gray, rather than that of the species-makers of recent years. This sanction is not in deference to authority, but for the reason that their species commend themselves to us. We prefer the Linnean idea of species not because it is Linnean, but because it is more useful than those proposed more recently. Probably one reason for the vogue of the Linnean conception of species for the past century and a half is that it is so well adapted to the mental requirements of botanists the world over. Linné was fortunate in adopting a measure of species which was neither so small as to be difficult to apprehend, nor so large as to be cumbersome. It may have been by happy chance that he hit upon this acceptable measure of species; it is much more likely that it was but another

example of that genius which gave him such great pre-eminence among the botanists of his day, and enabled him to make so lasting an impression upon systematic botany.

We have given a good deal of attention to the laws of botanical nomenclature, a matter of considerable, but by no means paramount, importance, while we have pretty largely neglected the far more important laws of botanical taxonomy. We have legislated at length in regard to names of species, genera, families, orders, and so on to the end of the list, while we have scarcely touched upon the far more important question of what these groups should be. We have been more concerned with the chaff than with the wheat itself.

We are forced to the conclusion that we have rather foolishly spent our time in discussing the less important matters of nomenclature, while we have permitted anarchy to thrive in the far more important work of the making of species. We have had botanical congresses which formulated laws in regard to the *naming* of species, but as to the *making* of species each botanist is allowed to follow his own notions without any guide whatever, and what is worse still, without any restrictions. The result is what we should expect. It is confusion; it is scientific anarchy. If an indefinite number of men were to contribute stones for a building, there being no agreement among them as to shape or dimensions, what would be the result? No worse, I am sure, than what has occurred in the erection of that portion of the edifice of science with which we are concerned to-day. It is almost incredible that we should have permitted the present condition of taxonomy to continue. Why mere tyros, wholly untrained in the underlying principles of the science of classification, should be allowed to contribute to the confusion of taxonomy is a matter which may well make us marvel. But there have been words of admonition. Nearly thirty years ago Dr. Gray in his "Botanical Text-book" spoke of the necessity of experience and

"the critical study of the classical botanical works," and then said "No one is competent to describe new plants without such study." Wiser words in regard to the question before us were never written, and had they been heeded during the past quarter of a century we should not have had the present condition of confusion in systematic botany. Certainly our practise of allowing everybody, whether trained for the work or not, to determine the limits of species is taxonomic anarchy.

It is increasingly evident that botanists must insist upon an adequate training by those who are proposing to make and describe new species. Every teacher of botany should impress his pupils with the seriousness of the work of making new species, and should train them to feel that such work should be left to the few who are masters in the subject. The rule which goes into effect to-day, requiring diagnoses of new species to be in Latin, will prove a deterrent to the tyros who would rush into print with their diffuse English descriptions. In this matter, at least, we should all uphold the Vienna code, and rigidly exclude as invalid all publication of species not conforming to it. A more effective deterrent could be provided by an agreement of botanists to restrict publication to certain botanical journals, whose editors should then exercise a revisionary control over all publication of new species. I am well aware of the objection that will be made to such a taxonomic censorship, but we have gone so far in the direction of individual liberty that it has degenerated into license, and some such drastic measure is loudly called for. When we had masters in botany, who were kings to whose authority all must bow, we complained bitterly. Now that the kings are dead the democracy of botany is suffering from the misrule of anarchy. If democracy will not control its subjects we shall have to return to a botanical oligarchy, or even to a dictatorship, for anarchy can not be endured.

Has not the time come for botanists to establish rules

governing and restricting the making of species? I am convinced that the next step forward in systematic botany must be the placing of limitations upon the men who are setting up new species, compelling them to conform their species to the conditions which make species necessary.

Of course this is not the time, nor is it the place, for final action in regard to this matter, and, moreover, I am certainly not the one to formulate rules for species-making, yet I may be allowed to suggest some botanical dicta or aphorisms as a short prodrome of a taxonomic code.

1. Taxonomy is a means, not an end; it does not exist for the taxonomists alone, but for the whole body of botanists.

2. The first purpose of classification is to include all individual plants in as small a number of species as possible.

3. That classification of the plants of the world most fully accomplishes its purpose which gives an adequate picture of the whole in the simplest form.

4. Species have been invented in order that we may refer to great numbers of individuals collectively, instead of singly; therefore the number of species must be far less than the number of individuals.

5. Since we make use of species for the purpose of saving labor in making the acquaintance of plants, it follows that those species whose limitations are so faint or vague that we apprehend them with difficulty have no reason for existence.

6. Scientific classification does not require that every difference in structure and habit be made the basis of a separate species. There must be room left for individual variation, otherwise we should have as many species as there are individual variations.

7. The taxonomist should look for resemblances rather than for differences, so that he may make fewer rather than more species.

8. Species must be so made as to be understood and appreciated by the botanists for whom they are described. A species has no legitimate reason for existence whose limits are perceptible only to its maker.

9. Experience must tell us what limitations of species are most convenient.

10. In making a species the guiding principle must be that it shall be recognizable from its diagnosis. A species that is not distinguishable by its diagnosis has no right to existence.

11. A diagnosis should be brief enough to be remembered readily, for this reason Linné's twelve-word diagnoses are worthy of imitation.

12. Long and complex descriptions should never be used for the limitation of species, and when such long and complex descriptions are found to be necessary this is a sufficient indication that the species should not be made.

These aphorisms are merely illustrative, and by no means cover the whole ground. Others will suggest themselves, especially to those of you who have been engaged in taxonomic work. It seems to me so desirable that a reform in taxonomy should be instituted that I venture to suggest that this society appoint a committee to report upon the feasibility of restoring species to their original importance and dimensions, the possibility of restricting species-making to those who are competent, and also of restricting publication to selected journals, thus involving some kind of taxonomic censorship.

THE TAXONOMIC ASPECT OF THE SPECIES QUESTION

DR. NATHANIEL LORD BRITTON

New York Botanical Garden

1. Historic

The ancients knew and described plants by generic names. Their knowledge of them was general and superficial. According to Adanson,[1] Conrad Gesner, 1559, was the first to indicate the distinction of plants into genera and species, although this advance is also claimed for Columna. Subsequent authors in general, for about a century, arranged species of plants under generic names, but without definite rules for the limitations of genera. Morison (1655), Ray (1682), and Tournefort (1694), defined genera with reference to their fruits and were followed by Linnæus.

Ray regarded specific differences as those that are somewhat notable and fixed and not due to cultivation and which cultivation does not change. The way to determine these, according to him, is to grow them from seed, because all the differences which are found in different plants grown from the same seed are accidental and not specific, but he was not always exact in following this rule.

Tournefort declared that it troubled him very little whether the plants he cited were species or varieties as long as they differed in remarkable and perceptible qualities; Adanson approves this view, remarking that it seems to him sufficient and reasonable.

From Linnæus, Philosophia Botanica, 1751.

We enumerate as many species as different forms were originally created.

[1] Fam. des Plantes 1: 102. 1763.

There are as many species as the Infinite Being originally produced different forms; and these forms, following the laws of reproduction imposed upon them, have produced more, but always similar to themselves. Therefore, there are as many species as there are different forms or structure met with to-day.

From Adanson, Familles des Plantes, 1763.

The moderns define a species of plant as a collection of several individuals which resemble each other perfectly, yet not in everything, but in the essential parts and qualities, without, however, giving attention to the differences caused in these individuals either by sex or accidental varieties.

According to Linnæus (Phil. bot., p. 99) "the species of plants are natural and constant, as their propagation either by seeds or cuttings is only a continuation of the same species. Individuals die, but the species does not."

But we wish to make a distinction between reproduction by seed and that by shoots, offsets, corms, cuttings, suckers or by grafting. These last simply continue the individual from which they are taken and consequently are opposed to the production of new species in plants; *whereas seeds are the source of a prodigious number of varieties, sometimes so changed that they may pass for new species.* He cites, among other examples:

"In 1715 Marchant found in his garden a new species of Mercurialis and the following year it came from self-sown seed; again, four resembled the parent and two were so different that he made another species of Mercurialis. These two new plants were cultivated and continued to grow each year."

It is well known that without foreign fecundation in plants that reproduce by seed, similar changes are induced either by reciprocal fecundation of two different individuals or owing to cultivation, the soil, the climate, dryness or moisture, light or shade, etc. These changes are more or less prompt, more or less durable, disap-

pearing in one generation or perpetuating themselves through several generations, according to the number, the force, the duration of the causes which united to form them, etc., according to the nature, the disposition, the customs, so to speak, of each plant, for it is to be noted that some families do not vary except in the roots, others in the leaves, others in height, pubescence, and color, whereas others change more easily their flowers or their fruit.

It is difficult to define a primitive species and which those are which have originated by successive reproduction or been changed by accidental causes. It is without doubt for this reason that we do not find nowadays a number of plants described by ancient botanists; they have disappeared, either by returning to primitive forms or by changing their form in the multiplication of species. For this reason the ancients knew fewer species; time has brought novelties! And for the same reason future botanists will be *overwhelmed* by the number of species and be obliged to abandon them and be *reduced solely* to *genera!*

From Lamarck, Encyclopedie Methodique, Vol. 2, 1786.

Species; in botany as in zoology, a species is necessarily constituted of the aggregation of similar individuals which perpetuate themselves, the same, by reproduction. I understand similarity in the essential qualities of the species, because the individuals which constitute it offer frequently accidental differences which give rise to varieties and sometimes sexual differences, which belong however to the same species, as the male and female hemp, in which all the individuals constitute the common cultivated hemp. Thus, without the constant reproduction of similar individuals, there could not exist a true species.

From Rees, Abraham, The Cyclopædia, Vol. XXXIII, 1819.

Species *of Plants*, in *Systematic Botany*, appear, as

far as can be ascertained from the universal experience of those who are conversant with them, as well as from everything that can be gathered from the records of remote antiquity, to remain distinct from each other, marked by their appropriate characters and qualities, and renewing themselves periodically by sexual generation. Such being the case with all the plants of which we have any knowledge, we conclude it to be so with the rest, as well as with animals. The white blackbird of Aristotle still inhabits the Cyllenian groves and copses of Arcadia, undisturbed by the revolutions of two thousand years; and we doubt not that the banks of the Alpheus have been fringed with the same violets and primroses, through uncounted ages, as those with which they are now, every spring, adorned.

Various plants indeed, and especially domestic ones, like domestic animals, are found liable to some variations of color, luxuriance, and sensible qualities, which have led curious inquirers to doubt whether any species are certainly permanent. This doubt could arise only from a slight view of the subject. Whatever casual aberrations there may be in the seminal offspring of cultivated plants, a little observation will prove how transient such varieties are, and how uniformly their descendants, if they be capable of producing any, resume the natural characters of the species to which they belong.

From A. P. DeCandolle and K. Sprengel, Elements of the Philosophy of Plants, Edinburgh, 1821.

By species we understand a number of plants, which agree with one another in invariable marks.

In this matter everything depends upon the idea of invariableness. When an organ, or a property of it, is changed neither by difference of soil, of climate, or of treatment, nor by continued breeding, this organ or property is said to be invariable. When, for instance, we have remarked during centuries, that the centifolia has always unarmed leafstalks, we say correctly, that this property of the centifolia is invariable.

This idea proceeds on the supposition that the species which we know have existed as long as the earth has had its present form. No doubt there were, in the preceding state of our globe, other species of plants, which have now perished, and the remains of which we still find in impressions in shale, slate-clay, and other flœtz rocks. Whether the present species, which often resemble these, have arisen from them; whether the great revolutions on the surface of the earth, which we read in the Book of Nature, contributed to these transitions—we know not. What we know is that from as early a time as the human race has left memorials of its existence upon the earth the separate species of plants have maintained the same properties invariably.

To be sure, we frequently speak of the transitions and crossings of species; and it can not be denied that something of this kind does occur, though without affecting the idea of species which we have proposed. We must, therefore, understand this difference.

We perceive the *Transitions of a Species,* when it loses or changes the properties, which we had considered as invariable in the character. Thus, it would be a transition, if we had stated as an invariable character of winter wheat (*Triticum hybernum*), that it was biennial, and had an ear without awns; and if we should remark, that by frequent reproduction, and by very different treatment, it began to assume awns, and, when sown in spring, came to maturity during the same summer.

But this shows only that our idea of the difference between the two kinds of grains had been incorrect; for it is the universal rule, that the character does not constitute the species, but the species the character. Species, then, only appear to undergo transitions, when we have considered an organ or a property as invariable which is not so.

All properties of plants which are subject to change, form either a subspecies or a variety. By the former we understand such forms as continue indeed during

some reproductions, but at last, by a greater difference of soil, of climate, and of treatment, are either lost or changed. When the different cabbage species receive the same treatment in the same climate, they continue to be frequently reproduced, without changing their appearance. But we can not on this account maintain, that cauliflower would retain the same favorite form in very different climates, and under a complete change of treatment. It at last changes so much, that it can scarcely be distinguished from the common cabbage. This, therefore, is a subspecies. Varieties again do not retain their forms during reproduction. The variable colors —the very variable taste, and other properties of the kitchen vegetables, the ornamental plants, and the fruit-trees, show what varieties are; and the scientific botanist must therefore be particularly attentive to distinguish permanent species from the variable subspecies, degenerate plants and varieties.

To this discrimination belongs, above all things, a careful, continued, and unprejudiced observation of the whole vegetation of the same plant during its different ages, and amidst the most different circumstances which have an influence on it. When, for instance, in the common *Lotus corniculatus,* on whatever soil it may grow, we uniformly observe that it has a solid stem, even and erect divisions of the calyx, and expanded filaments, we must of necessity distinguish, as a particular species from it, another form which grows in bogs and in watery meadows, which has a much higher, and always hollow stalk, the divisions of its calyx spread out into a star-shape and hairy, and which has uniformly thin filaments; and we must name this latter species either *Lotus uliginosus* with Schkuhr, or *Lotus major* with Scopoli and Smith. As, on the other hand, the *Pimpinella Saxifraga* grows sometimes quite smooth, and sometimes in woods and shady meadows, considerably hairy; as it displays sometimes simple and small stem-leaves, sometimes half and even doubly pinnated leaves; and as these

forms vary according to the situation of the plant and during reproduction, we can not regard these forms by any means as distinct species, but we must view them as corruptions.

We see, that, in order to decide respecting the idea of a species, an observation of many years, and of much accuracy, is often required; and that the cultivation of plants, from the most different climates, in botanical gardens, is in the highest degree necessary for their discrimination.

From Lindley, John, An Introduction to Botany, London, 1832.

A *species* is a union of individuals agreeing with each other in all essential characters of vegetation and fructification, capable of reproduction by seed without change, breeding freely together, and producing perfect seed from which a fertile progeny can be reared. Such are the true limits of a species; and if it were possible to try all plants by such a test, there would be no difficulty in fixing them, and determining what is species and what is variety. But, unfortunately, such is not the case. The manner in which individuals agree in their external characters is the only guide which can be followed in the greater part of plants. We do not often possess the means of ascertaining what the effect of sowing their seed or mixing the pollen of individuals would be; and, consequently, this test, which is the only sure one, is, in practice, seldom capable of being applied. The determination of what is a species, and what a variety, becomes therefore wholly dependent upon external characters, the power of duly appreciating which, as indicative of specific difference, is only to be obtained by experience, and is, in all cases, to a certain degree arbitrary. It is probable that, in the beginning, species only were formed; and that they have, since the creation, sported into varieties, by which the limits of the species themselves have now become greatly confounded. For ex-

ample, it may be supposed that a rose, or a few species of rose, were originally created. In the course of time these have produced endless varieties, some of which, depending for a long series of ages upon permanent peculiarities of soil or climate, have been in a manner fixed, acquiring a constitution and physiognomy of their own. Such supposed varieties have again intermixed with each other, producing other forms, and so the operation has proceeded. But as it is impossible, at the present day, to determine which was the original or originals, from which all the roses of our own time have proceeded, or even whether they were produced in the manner I have assumed; and as the forms into which they divide are so peculiar as to render a classification of them indispensable to accuracy of language; it has become necessary to give names to certain of those forms, which are called species. Thus it seems that there are two sorts of species: the one, called natural species, determined by the definition given above; and the other, called botanical species, depending only upon the external character of the plant. The former have been ascertained to a very limited extent; of the latter nearly the whole of systematic botany consists. In this sense a species may be defined to be "an assemblage of individuals agreeing in all the essential characters of vegetation and fructification." Here the whole question lies with the word essential. What is an essential character of a species? This will generally depend upon a proneness to vary, or to be constant in particular characters, so that one class of characters may be essential in one genus, another class in another genus; and these points can be only determined by experience. Thus, in the genus Dahlia, the form of the leaves is found to be subject to great variation; the same species producing from seed, individuals, the form of whose leaves vary in a very striking manner; the form of the leaves is, therefore, in Dahlia, not a specific character. In like manner, in Rosa, the number of prickles, the surface of the fruit,

or the surface of their leaves, and their serratures, are found to be generally fluctuating characters, and can not often be taken as essential to species. The determination of species is, therefore, in all respects, arbitrary, and must depend upon the discretion or experience of the botanist.

From Nicholson, Henry Alleyne, A Manual of Zoology, New York, 1876.

Species.—No term is more difficult to define than "species," and on no point are zoologists more divided than as to what should be understood by this word. Naturalists, in fact, are not yet agreed as to whether the term species expresses a real and permanent distinction, or whether it is to be regarded merely as a convenient, but not immutable, abstraction, the employment of which is necessitated by the requirements of classification.

By Buffon, "species" is defined as "a constant succession of individuals similar to and capable of reproducing each other."

DeCandolle defines species as an assemblage of all those individuals which resemble each other more than they do others, and are able to reproduce their like, doing so by the generative process, and in such a manner that they may be supposed by analogy to have all descended from a single being or a single pair.

M. de Quatrefages defines species as "an assemblage of individuals, more or less resembling one another, which are descended, or may be regarded as being descended, from a single primitive pair by an uninterrupted succession of families."

Müller defines species as "a living form, represented by individual beings, which reappears in the product of generation with certain invariable characters, and is constantly reproduced by the generative act of similar individuals."

According to Woodward, "all the specimens, or individuals, which are so much alike that we may reasonably

believe them to have descended from a common stock, constitute a *species*."

From the above definitions it will be at once evident that there are two leading ideas in the minds of zoologists when they employ the term species; one of these being a certain amount of resemblance between individuals, and the other being the proof that the individuals so resembling each other have descended from a single pair, or from pairs exactly similar to one another. The characters in which individuals must resemble one another in order to entitle them to be grouped in a separate species, according to Agassiz, "are only those determining size, proportion, color, habits and relations to surrounding circumstances and external objects."

On a closer examination, however, it will be found that these two leading ideas in the definition of species—external resemblance and community of descent—are both defective, and liable to break down if rigidly applied. Thus, there are in nature no assemblages of plants or animals, usually grouped together into a single species, the individuals of which *exactly* resemble one another in every point. Every naturalist is compelled to admit that the individuals which compose any so-called species, whether of plants or of animals, differ from one another to a greater or less extent, and in respects which may be regarded as more or less important. The existence of such individual differences is attested by the universal employment of the terms "varieties" and "races." Thus a "variety" comprises all those individuals which possess some distinctive peculiarity in common, but do not differ in other respects from another set of individuals sufficiently to entitle them to take rank as a separate species. A "race," again, is simply a permanent or "perpetuated" variety. The question, however, is this —How far may these differences amongst individuals obtain without necessitating their being placed in a separate species? In other words: How great is the amount of individual difference which is to be considered

as merely "*varietal,*" and at what exact point do these differences become of "*specific*" value? To this question no answer can be given, since it depends entirely upon the weight which different naturalists would attach to any given individual difference.[2] Distinctions which appear to one observer as sufficiently great to entitle the individuals possessing them to be grouped as a distinct species, by another are looked upon as simply of varietal value; and, in the nature of the case, it seems impossible to lay down any definite rules. To such an extent do individual differences sometimes exist in particular genera—termed "protean" or "polymorphic" genera—that the determination of the different species and varieties becomes an almost hopeless task.

The second point in the definition of species—namely, community of descent—is hardly in a more satisfactory condition, since the descent of any given series of individuals from a single pair, or from pairs exactly similar to one another, is at best but a probability, and is in no case capable of proof.

Upon the whole, then, it seems in the meanwhile safest to adopt a definition of species which implies no theory, and does not include the belief that the term necessarily expresses a fixed and permanent quantity. Species, therefore, may be defined as *an assemblage of individuals which resemble each other in their essential characters, are able, directly or indirectly, to produce fertile individuals, and which do not (as far as human observation goes) give rise to individuals which vary from the general type through more than certain definite limits.* The production of occasional monstrosities does not, of course, invalidate this definition.

From Gray, Asa, Structural Botany, Ed. 6, 1879.

Species in biological natural history is a chain or series

[2] As an example of this, it is sufficient to allude to the fact that hardly any two botanists agree as to the number of species of willows and brambles in the British Isles. What one observer classes as mere varieties, another regards as good and distinct species.

of organisms of which the links or component individuals are parent and offspring. Objectively, a species is the totality of beings which have come from one stock, in virtue of that most general fact that likeness is transmitted from parent to progeny. Among the many definitions, that of A. L. Jussieu is one of the briefest and best, since it expresses the fundamental conception of a species, *i. e.,* the perennial succession of similar individuals perpetuated by generation.

The two elements of species are: (1) community of origin; and, (2) similarity of the component individuals. But the degree of similarity is variable, and the fact of genetic relationship can seldom be established by observation or historical evidence. It is from the likeness that the naturalist ordinarily decides that such and such individuals belong to one species. Still the likeness is a consequence of the genetic relationship; so that the latter is the real foundation of species.

No two individuals are exactly alike; and offspring of the same stock may differ (or in their progeny may come to differ) strikingly in some particulars. So two or more forms which would have been regarded as wholly distinct are sometimes proved to be of one species by evidence of their common origin, or more commonly are inferred to be so from the observation of a series of intermediate forms which bridge over the differences. Only observation can inform us how much difference is compatible with a common origin. The general result of observation is that plants and animals breed true from generation to generation within certain somewhat indeterminate limits of variation; that those individuals which resemble each other within such limits interbreed freely, while those with wider differences do not. Hence, on the one hand, the naturalist recognizes *varieties* or differences within the species, and on the other *genera* and other superior associations, indicative of remoter relationship of the species themselves.

From Darwin, Origin of Species, new edition, from the sixth English edition, New York, p. 33, 1883.

No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species. . . . The term variety is almost equally difficult to define; but here community of descent is almost universally implied, though it can rarely be proved.

From Britton and Brown, Illustrated Flora **1**: VI., 1896.

A species is composed of all the individuals of a kind capable of continuous successive propagation among themselves.

From De Vries, Species and Varieties, p. 32, 1905, under Elementary Species in Nature.

"What are species?" Species are considered as the true units of nature by the vast majority of biologists. They have gained this high rank in our estimation principally through the influence of Linnæus. They have supplanted the genera which were the accepted units before Linnæus. They are now to be replaced, in their turn, by smaller types, for reasons which do not rest upon comparative studies but upon direct experimental evidence.

2. Discussion

Any method of evolution makes difficult the establishment as a general conclusion, that all the progeny of a species must belong to that species. The paleontologists have always faced this difficulty; their species have of necessity been assumptions, and theoretically, at least, if the complete representation of any line of descent could be assembled it would be seen at once that the whole series of forms were in some way connected. The induced mutation effected by MacDougal in *Raimannia odorata,* in which plants so different from their immediate parent as to appear, at least, specifically distinct

from it, as compared with other feral species, is a notable addition to the difficulty of maintaining such a conclusion.

As long as species were generally understood to be relatively fixed in characters, their delimitation was relatively simple, but the general understanding that all living organisms are descended from others which were different from them has greatly complicated the subject.

Whether the evolution has been by imperceptible progressive modifications of structure, or by mutations, or by both methods, the result is essentially the same from the practical standpoints of taxonomy; from these standpoints, then, similarity of individuals must remain the consideration to which most weight will be given in taxonomic usage. It has been conclusively proved that many mutants and elementary species or races breed true in enough instances to establish the rule for at least a number of generations; this should not, however, in my opinion, admit them to the category of species, which, though necessarily difficult in delimitation, will still remain the practical taxonomic groups, recognizing, nevertheless, that they are made up of either relatively constant or of widely fluctuating elementary components, which, in turn, will presumably yield the species of future geologic ages.

The recognition of the existence of incipient or elementary species or races within the composition of species, explains, in large part, the multiplication of species and of groups of assumed lower rank, in many of the larger genera, nearly every taxonomist, except the most conservative, having taken more or less part in thus increasing the number of descriptions and of names. They have been variously denominated species, subspecies, varieties, subvarieties and forms, according to the point of view of the investigator.

Geographic distribution has been invoked as a very useful aid in determining the limits of species. It is a well-recognized fact that certain areas of the earth's surface, some large, some small, are characterized by types

of plants which differ from those of other areas, either contiguous or widely separated, and, in cases where types inhabiting different areas so characterized are apparently similar, though different, their separation or isolation has been given weight in regarding them as specifically distinct. No doubt this is a rational course to pursue if it is not carried to extremes. The question whether the environments to which the ancestors of such types have been exposed have been the cause of their differentiation, or whether the elementary species have been perpetuated which were best adapted to the soil, climate or other features of the environments, is one of the most interesting of unsolved problems. That similar types have for the most part come from common ancestors we must regard as most probable, even if now inhabiting widely separated regions, segregated by the disappearance of related types in intervening space, being thus remnants of the more general distribution of the ancestral forms in earlier geologic eras.

Geographic distribution must, however, in cases of contiguous land districts, be cautiously used as a determining factor. There are many instances in which a species with certain well-marked characters in one region is, apparently, at least, completely connected through intermediate characters with what is readily regarded as a perfectly distinct species in another region. Instances of this kind are within the experience of every one who has given attention to geographic distribution of plants. I say this is apparently the case; the conclusion is based on long series of herbarium specimens and on field observations made over large areas of country. Neither of these methods of information is wholly satisfactory, because the herbarium series must necessarily be limited in the number of specimens, and also because the field observations have to be taken at different times and usually at widely separated intervals. Still, the consensus of opinion of plant geographers leans strongly to the existence of intermediate forms in intermediate regions.

Some of these are almost certainly hybrids, but it would not be safe for us to conclude that they all are. Some light has been thrown on this question by the growing of the extreme forms side by side, and more information can doubtless be thus obtained, the principal difficulty being that the environment of the one is often fatal to the other. A better method would be to grow the two apparent extremes within the natural environment of the apparent intermediates.

3. The Taxonomic Treatment of Groups assumed to be of Lower Rank than Species

There is perhaps no taxonomic subject on which greater diversity of opinion and practise exists than in the arrangement and nomenclature of groups of individuals not accorded full specific value. The relationships of these groups to the group assumed to constitute the species proper, and the nomenclature of these subsidiary groups, vary all the way from regarding them all as species, to regarding some of them as subspecies, some as varieties, some as subvarieties, others as forms, while even finer distinctions have been attempted, and elaborate monographs of many genera have been written in the attempt to express descriptively these interrelationships. It has been very evident that these described groups are of unequal value, some resembling the assumed typical group more, some less, and in a good many instances very little. The general result of these attempts to dissect nature has been embarrassing, because when a subsequent student takes up the group he is wholly unable to determine from any descriptions that can be written where any given individual would have been grouped by the previous author, unless he has access to the actual specimens which the previous author studied, and the subsequent student also finds that the examination of a large number of different individual specimens from those studied by his predecessor contains some which

do not fully agree with any one of his predecessor's descriptions, or he finds that some of his specimens agree about as well with one of the groups recognized by the previous author as they do with another. This result shows conclusively that for practical taxonomic purposes it is not desirable to attempt to define a great many of these minor groups. The tendency has been brought about, I believe, by the instinct of many investigators that everything in nature must be named and described, but nothing is to be gained by permitting this laudable purpose to run to extremes.

It is evident, I think, that our taxonomy has been based on the fundamental error that the plant world is to be regarded as divisible into smaller and smaller groups, rather than following nature and proceeding on the theory that it is built up of greater and greater ones; the science should be synthetic rather than analytic. The synthetic theory will give our observation and experimentation a different significance and enable us to comprehend some of the phenomena now masked by the analytic method of attack.

If, as now seems more probable than a few years ago, species are made up of elementary species, or races, and that these are being increased by mutation, there can be no end to the number of such groups produced. As to the designation of these groups, I suggest that the term race be employed. This has long been used to designate what have been called self-perpetuating varieties, which appear to me to be identical with the present conception of elementary species, and its application may readily be widened. The term variety loses its significance, because it is usually quite impossible to tell how any given individual or group of individuals has arisen, or from which species it has sprung. The term form could be used instead of either race or elementary species, but it has had such a trivial significance in literature that race seems to be preferable. Subspecies implies divisibility, and is, therefore, an undesirable term.

In conclusion, I submit the following propositions:

1. The individual is the taxonomic unit, usually undesignated.

2. Similar individuals constitute a race.

For general taxonomic purposes races need not be designated; the conception and description of the species is broad enough to include all races of which it is composed. There will never be complete uniformity of agreement as to the distinction between races and species, any more than there will ever be complete agreement as to the limitations of genera. It is futile in science to attempt to lay down principles which interfere with individual judgments. For special purposes the races may be designated numerically, as, *Quercus alba,* race 2; *Œnothera biennis,* race 12; *Bursa Bursa-pastoris,* race 17; *Draba verna,* race 104. There are doubtless many instances where the species is composed of only one race, just as we have monotypic genera composed of but one species.

3. Similar races constitute a species, the species designated binomially.

4. Similar species constitute a genus, the genus designated monomially.

THE PHYSIOLOGIC ASPECT OF THE SPECIES QUESTION

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NOT being sure of what ground might already be covered by the speakers who have preceded me on the program, I take the liberty of presenting my matter after giving thought to what has been said; and I find in mentally reviewing this—that the species concept as presented by the previous speakers does not embrace the whole field as it is forced upon me in my every-day work. I am especially surprised at this, because the first speaker, under whom I secured my elementary training in botany, is very particular in giving instruction to his pupils to begin with the one-cell plant and to work up from the simple to the complex. Yet, so far as I could ascertain in listening most carefully, he has not now taken into consideration a single one of the simple plants of which he knows there are many thousand times as many as there are of flowering plants, therefore I seem to be left somewhat adrift for my presentation.

I will not attempt to give any historical aspect of the question, but to take it up from the point in which it appeals to me in my every-day work, for it is a problem that I have been obliged to meet, and as I have met it, I will present the results to you.

As I understand it, we are taking up the question of the species concept. I thought it quite well worth while, in looking up the matter, to see what a man who has entirely changed the aspect of the subject within not so very many years might say as to what he considered a species concept, and so I very carefully again looked through my copy of Darwin's "Origin of Species." If

a man were going to revolutionize the world of thought he certainly, I assumed, would give a definition of the subject he is going to treat. But I could not find a word as to what Darwin meant by species. He writes as if all the world knew what species are. Yet I did find this in the latter part of the last chapter; he says, "And now we shall be freed from the vain search for the undiscovered and undiscoverable essence of the term species." Consequently, here we are, tracing a will-o'-the-wisp. And yet, it seems to me, there must be something that we are all thinking about when we say species. There must be some workable idea. Of course I know that since Darwin's time and the vast accumulation of knowledge in reference to heredity and variation, to say nothing about other physiological aspects proper, our ideas have decidedly changed. Still, as I look over the actual work being accomplished in determining the number and the extent of the species of plants in the world, I do not see that our practise especially differs from the pre-Darwinian practise. We have a theoretical idea of what species are, but practically we describe them for the most part in the same pre-Darwinian terms, the really Linnean terms, so far as many of us can, although we do not adhere to the Linnean brevity. Nevertheless, there are some instances in which it seems necessary to deviate from this practise, if we wish to handle our subject in such a way as to make it useful; for I assume, in the first place, that whatever the species concept may be, it is something which enables us to present ideas or problems in a better form than we could otherwise accomplish. At any rate, the idea of a species is a mental tool of some sort.

To take up the purely physiological aspect; possibly it was the study of bacteria which forced this phase of the question upon us for the first time. I judge that it came largely from the fact that bacteria are so very minute. What could one do if he were going to describe the thousands of species of bacteria simply as plants,

with genera and life history as in the case of other plants? In the first place, morphological characters are too ill-defined, if indeed they exist, and so he was forced to devise some other means of discrimination. This means was at first almost purely physiological. It largely depended upon the behavior of the individual sorts, or the groups of individual sorts, to certain nutritive processes. It depended upon what kind of media the bacteria grow upon, the temperature, and access to oxygen. Upon these physiological results in large part have been built our vast knowledge, economic very largely, of the many kinds of bacteria which are designated as species. But we may pass by the bacteria for a time and take up the larger organisms. I think the ones that are most useful in this connection are the strictly parasitic forms.

There is no more interesting and better understood group at the present time than the plant-rusts. The forms are sufficiently large to furnish a variety of species and genera exhibiting morphological characters, and yet, being strictly parasitic, are particularly restricted by the nature of the substratum. I will give one or two instances to illustrate. There is a group of forms—I will admit that I hardly know what terms to use in speaking of them, but I will say a group of forms—which grow upon the various species of Carex. It is found that by taking rust spores from a single host of any particular Carex and sowing them upon an Aster, or a Solidago or an Erigeron, they will grow upon one of these genera, it makes not much difference what the species, but not upon the other two. Now if spores are taken from another Carex, the spores being so exactly like the former that they can not be distinguished by any visible characters, and sown upon plants of the same three genera, they may grow upon a different one than in the former instance, but not upon the remaining two. Thus finally we will get three sets of forms, one growing on Aster, one on Solidago and one on Erigeron, which can not be

made to interchange, although they possess no evident morphological differences. This result depends, as I assume and as seems to be pretty well authenticated by all the researches, upon a question of nutrition. It does not depend upon any peculiar structure of Aster, Solidago or Erigeron; but here we have three genera which furnish different kinds of nutritive matter, or in some way differently affect the nutrition of the fungus, so that a fungus which has adapted itself to live upon one of these generic groups of plants will not live upon, or can not live upon, the other. It is a very nice adjustment to a particular kind of nutriment; I think we are quite well assured of that fact.

Now, the question arises, are these three species? If you choose to look up the literature, you will see that the speaker has described them as three species under three independent names. That does not mean that he believes they are truly three species, but that it was a convenient way of designating the three physiologically different kinds until a time when the matter could be more fully considered. Now, are these three species? Well, to confess to you, not to say it too loudly, I do not believe they are. They are not three species in the generally accepted sense because they can not be distinguished morphologically. What then is, or should be, our conception of a species? Is it something to be distinguished physiologically or morphologically, or in both ways? This is not a hypothetical question, because the literature of the subject that I represent is very full of descriptions of species based entirely or partially upon physiological data, and I am assured that we are not alone in this method of describing species.

If I understand aright, the ornithologists, at least some of them, are willing to assert that species may differ by characters which can not be described by words [laughter]; that is to say, you will know the species when you see it, but you can not describe it in any language by which another person may recognize it. I

think that this is not a joke, but that it is really stated in earnest; because, I read it in *Science*. [Laughter.] But I fancy botanists have not gone quite that far.

Now, just another instance that arose during an extensive series of culture studies; that is the case of the Helianthus rusts. They have been described according to the host plants on which they grow. Each species of Helianthus and its close relatives appear to bear a distinct kind of rust, which acts in cultures as if it were an independent species. Yet any and all of these will grow on Helianthus annuus, a so-called bridging host. Are these different species different biological or physiological species, or simply forms or races? Possibly it would be well to refer them to some sub-category, as Dr. Britton has suggested.

I think when we come to study other parasitic forms thoroughly we shall find this condition equally true, for instance, in the genus Cuscuta among flowering plants. Furthermore it is probably true in many cases of plants which are not parasitic. We had an illustration this morning in the cultures of Penicillium exhibited by Dr. Thom, where characters of taxonomic importance were developed according to the medium on which the fungus was grown.

It seems highly probable that a physiological cause for variation, which may be considered as specific under many circumstances, could be traced throughout the vegetable kingdom. For purposes of study I assume that in most cases of physiological species, they may develop in the course of time into true taxonomic species, having distinct morphological characters, and that in cases such as I have enumerated, we are dealing with nascent species. The rules which have been laid down in the presentation of the subject by the previous speakers apply more particularly, I think, to forms well differentiated morphologically. But due recognition should be given to forms of physiological origin, as I have shown. Finally, I would say, at least it is a rule

which I have formulated for my own guidance—it was a necessity that I should formulate some rule—that species, which are concepts, as I take it, for our convenience in discussing the various questions pertaining to plants, should be distinguished by sufficient morphological characters, the distinctions based upon physiological differences having subspecific rank. What constitute sufficient morphological characters must be left to the individual judgment.

THE PHYSIOLOGICAL ASPECT OF A SPECIES

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The simple recognition of different kinds of plants must be of great antiquity, and perhaps no single idea affords a better index of scientific thought during the last few centuries than the species conception. The occasion does not warrant a detailed statement of its development farther back than the time of Linnæus, who gave the idea a distinctly morphological stamp which it has retained to the present day. His systematization of natural objects marked the beginning of a period in which the morphological view of nature has prevailed throughout, the mechanics of form reaching its very apotheosis in the writing of De Candolle, De Bary, Hofmeister, Schwendener and a score of other eminent investigators who have triangulated the field of natural history of plants, basing relationships and constructing systems of phylogeny upon pure form, and upon the mechanical relations of cell-structure.

A century since, the ideas of continuing origination and endless evolutionary change took on definiteness and clearness with the writings of Lamarck, and this has grown until a distinctly vitalistic and genetic view-point has been gained, with the inevitable rearrangement of perspectives and modifications of conclusions as to the groupings and manner of relationships among living things.

Latterly, after statistical methods had reached a state of fair efficiency, their introduction into the study of occurrence, characters, distribution and form, has resulted in leading consideration from the type or the individual, to aggregates, or to the whole mass of individuals

of a group, by which amplitude of variation and mode of ontogenetic procedure may be accurately outlined.

The development of this aspect of natural history has been followed by a truer estimation of capacities and activities as attributes of organisms, with the result that even morphology has come to be based upon physiological principles, upon which alone it may make further material progress.

The groups with which the physiologist deals in the detection of activities, estimations of functions and measurements of performance, consist of a series of generations of individuals through which identical qualities, characters and capacities are transmitted uniformly within the limits of fluctuating variability. These groups may sustain the most diverse relationship and all possible degrees of affinity, but differ essentially in their physiological response to any given environment under permanent existence in it.

To test such conceptions of hereditary entities implies pedigreed cultures, or observations upon lineal series under known conditions of descent, hybridization operations and statistical estimations. The various qualities do not display themselves equally throughout the metameres of the sporophyte, and it is by no means to be assumed that the flower, or the terminal portion of the shoot surviving at maturity, is a compendium of the various developmental stages. Nowhere is this more beautifully apparent than in intermediate hybrids of the first generation, in which the qualities of one parent predominate in the leaves and the other organs of the first, or lower internodes, while those displayed by the upper terminal portions of the stem and flowers may be those of the other parent. Exemplifications of this fact have also been observed, in which the internodes and the organs formed during the first season's growth in two nearly related forms were widely different, displaying divergent structures and different "nasties" and tropisms. During the second year's growth, the organs formed

would be so nearly alike as to be in themselves inadequate for the separation of the two by ordinary taxonomic methods. These facts, which have been illustrated more than once in my own cultures, are quite at variance with the supposition that closely related forms are most alike in the seedling and younger stages and most divergent in the members of the adult formed latest.

Another form of transgressive variability is found when some descendants of individuals belonging to strain A, are apparently but little separated from B. Morphologically this would appear as an intergradation, but in reality the resembling individuals are divided and divisible into two groups, each carrying its own inherited potentialities, and in their progeny arranging themselves more or less symmetrically around the form of the strain, race or species. That the inclusion of the two is widely different may be illustrated in a striking manner by their action when crossed by a third form.

It can not be maintained that taxonomic thought has accurately or quickly reflected these modern estimations of the nature of living forms, for the very magnitude of the system necessary for the expression of relationships operates to prevent anything like a rapid or accurate adjustment.

Taxonomy is an eminently practical phase of botany, and it may reach its greatest general and total usefulness by confining its practise to the delineation of readily appreciable entities whether they be "natural" or "artificial."

So far as investigation in genetics and in the general functional activities of plants is concerned, however, progress is to be made only by increasing precision of measurement, and refined exactness of method of estimation of the qualities and characters concerned in the activities of the organism in both heredity and functional performance. The realization of this requirement comes but slowly. There are writers who still insist that the intricate pattern woven by the plant during its ontogeny,

as determined by micrometric measurements, developmental observations, experimental tests and statistical estimations upon the aggregate of the group, shall be capable of demonstrations by the foot rule and hand lens applied to the apical structures exhibited by a single individual of the mature sporophyte, as if the pedometer and hand compass were adequate for testing the results of a triangulation made by the transit and steel tape. In other words, botanists of academic habit will with the greatest gravity attempt to read out of existence, and estimate of no importance, hereditary groups of organisms unless they conform to certain illy defined arbitrary standards.

Taxonomic thought rounds its broadest conceptions when its conclusions are based upon the aggregate of individuals within natural groups, and embody ontogenetic procedure, environmental relations, heredity, evolutionary change and comparative functional performance. So organized it might rightly lay claim to being "philosophical botany," and would include an orderly arrangement of all knowledge of plants, and would form the basis upon which all researches might be founded.

Taxonomic practise is quite another matter; hampered as it is by an outworn and mediæval method of giving names to living organisms, it is doubtful as to how far we might demand of it that it discriminate among the many degrees of relationship which reveal themselves in capacities and performance as well as in refinements of form. The more thoroughly and accurately however, that it takes into account the total sum of the attributes, qualities and capacities of the plant, the greater will be the value of its conclusions, and the greater will be the service it may render to coordinate branches of botanical science.

AN ECOLOGIC VIEW OF THE SPECIES CONCEPTION

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I. Past and Present Practise in Species-making

The species may be either a means or an end; properly it is both. In descriptive botany, these two uses of the species have often been confused. The describing of new species has come to be recognized as an end in itself, while it should be nothing more than a necessary preliminary to further and more important botanical study. The interest of the ecologist in the proper recognition and naming of species is necessarily greater than that of nearly all other botanists. To him species are an indispensable means in the study of vegetation. On the other hand, the search for the definite results of adaptation and evolution, which is his final work, leads him inevitably to the species as an end. It is this double significance of the species for the ecologist that makes him peculiarly concerned about its treatment. So long as he uses the species only as a means, he is not greatly confused, except as a consequence of the fact that species are habitually made in the herbarium upon a small number of specimens, while he meets them as hundreds and thousands of variable individuals. His serious troubles begin with experimental work in adaptation and evolution. It quickly becomes evident that species so-called are widely different in rank, origin and relationship. Some are clearly species in the usual sense, while others are merely variations and forms of these. The ecologist thus comes to look with doubt upon all species. He accepts them reluctantly and provisionally until they meet successfully the test of experiment.

Even a casual survey of the practises in species-making during a century or more shows little or no uniformity of criteria or results. A comparison of methods in the different plant groups is even more striking. This lack of uniformity is found not only in the work of botanists in general, but even in the work of the same botanist. The consequences in the form of unequal and invalid species have been almost innumerable. This is particularly true of the fungi. To one familiar with them, it seems certain that the number of valid species is considerably less than half the number published. Attempts to guide the descriptive botanists and to make species more definite and uniform have not been wanting. A few of these have been noted, in order to show how little effect they had, even upon their own authors, and how utterly impossible of application they are without the test of experiment.

The criteria proposed by Ray were permanence of form and appearance, and non-fertility with other species. This appears to be little more than an attempt to justify the practise prevalent under the dogma of special creation. Mere observation could give little support to either criterion, and the thought of experimental support was scarcely dreamed of. As a pioneer in evolution, Lamarck gave a definition of the species, which would be expected to warrant more than passing interest. He defined a species as a "collection of similar individuals which are perpetuated in the same conditions as long as their environment is not changed sufficiently to bring about variation in their habits, their character or their form." It is clear that the whole value of this definition depends upon the significance given to the word variation. Lamarck, in his strong feeling for adaptation, hit upon the two essential facts, environment and variation, but his application of these criteria was purely academic.

It is a significant fact that Darwin should have written the "Origin of Species" without pointing out just what he meant by a species. His task was to prove origin

by descent as opposed to origin by special creation. For this purpose, it was unnecessary as well as impossible to define a species or to discover the method by which it originates. Darwin regularly used the terms species, subspecies and variety, but he did not draw a definite and constant line between them. De Vries has taken the first definite step in advance by the use of experiment to determine a species. It remains to be seen whether his concept of elementary species will clarify or confuse. It can not be accepted even provisionally until much more experimental work has been done.

In the last decade or two, conservative American botanists have often expressed the view that proper specific characters can be drawn only from the flower and fruit, or from the reproductive parts, whatever they may be. Since this has sometimes been said to have been Dr. Gray's view also, it seemed that it would be both profitable and interesting to compare the criteria of conservative and radical describers of species in the same family and genus. Time was lacking for a thorough and complete comparison, but in the few families selected the results seem representative. It was quickly seen that many current species accepted by all were not based upon reproductive characters, and that some of the most doubtful of recent ones were. It further appeared that, while habit, leaf, stem, etc., played slightly more important parts in later work, there was little essential difference in the kind of criteria used. The striking difference lay in the fact that the new species segregated are based upon much smaller variations of the parts concerned, as a rule, and are consequently much more difficult to distinguish when represented by many individuals.

The ecologist finds it a necessity to be able to distinguish and to refer to any difference represented by a number of individuals. A form or a variation is just as important to him as a species, and often presents a better point of attack. He must consequently be partly in sympathy with the present tendency of descriptive bot-

any to search out and describe all groups that are different, regardless of the degree of difference. He must, however, know the relationship of these groups, *i. e.*, whether they are coordinate species, forms or what not. To publish them all as binomials regardless of their rank completely hides their relationship to species already in existence. It is easy to understand that this has resulted partly from the fact that a trinomial is longer and hence less convenient than a binomial. Convenience is much less essential than accuracy and clearness, and must eventually yield to permit the regular use of the trinomial to designate the various differentiations of a species. The treatment of all groups below the genus as essentially coordinate is due even more to the fact that questions of ancestry and of origin enter all too rarely into the making of new species. These are questions that can be settled only by the most extensive and intensive field work, followed by thorough experiment. For such work there has as yet been almost no time or sympathy, as is shown by the all but hopeless mélange of so-called new species.

II. Bases for Distinguishing Species

The universal basis for distinguishing species has been the degree of morphologic difference. Physiologic and ecologic differences have but rarely been taken into account, except in such groups as the bacteria. The morphologic treatment is based upon the fundamental fact that stable structures are ancestral, and plastic ones derived. This has led to the basic principle that reproductive characters are of greater worth than vegetative ones. With this the ecologist is in full accord theoretically, but he would wish to have experimental evidence before accepting it as universally true. In fact some of the little evidence at present available indicates that this rule must permit some exceptions. It must constantly be borne in mind, especially by those who believe that evolution is always a question of the germ-plasm, that

vegetative features alone are present in the blue-green algæ and many of the fungi. It is evident that the method of morphologic differences greatly facilitates the provisional cataloguing of a flora, but it suffers from a universal and serious fault. This is the use of a few herbarium specimens in lieu of a large number of field individuals. Practically every collector selects a few individuals that appear typical, while for the purpose of scientific species-making he should collect as complete a series as possible of divergent individuals. Even if this were done, the ecologist must continue to regard the method as a mere preliminary, which serves to arrange the material and hence to facilitate the real study of species.

Closely connected with morphologic difference is the question of the absence of intermediate forms. This appears to have played a more important part in zoology than in botany. In the latter case, at least, it seems often to have been taken for granted as a necessary consequence of structural differences. At best, it has regularly been a question of intermediate forms in the herbaria and not in the field.

Constancy as a criterion of species is also but another phase of morphologic difference. As such it seems to have been used chiefly to designate uniformity of difference throughout the individuals concerned. The constancy of a structure from one generation to another, or from one habitat to another has been given little attention in species-making. Yet it is precisely these which are of fundamental importance. This fact, however, makes it at once evident that constancy is something that can only be determined by combining the most extensive field observations year after year with experiments in various habitats. This makes it clear that our present knowledge of constancy is almost purely theoretical, and that it is profitless to discuss it in our present ignorance of it.

To the ecologist, then, the usual bases for distinguish-

ing species, viz., degree of morphologic difference, absence of intermediate forms, and constancy, are entirely inadequate. He sees three critical facts in the development of a new species or any new form: (1) ancestry, (2) habitat or method of origin, (3) structural changes, very rarely functional ones. None of these can be studied adequately anywhere but on the ground. The first two are purely experimental questions. While the most thorough field study is a necessary preparation for them, they can never be decided except by experimental methods in the field. Apart from the study of the origin and structure of vegetation, the fundamental task of the ecologist is the experimental investigation of the origin of new forms, the so-called species.

III. Ecologic Procedure

The questions of what a species is, what are species and what are not, and of the origin of species and of forms must then be decided by experiment. The method of attack is easily determined, but the procedure is superlatively slow and laborious, and the demand upon time and patience unlimited. In spite of his inclination, the ecologist finds it necessary to accept as a working basis the species at present distinguished. His first task is to discover those that seem to give the best promise of results under experiment. The procedure consists of two essential processes: (1) field observations throughout the habitat of the species concerned and (2) experiment. The latter is the crux of the whole question. It consists of three steps: (1) the exact measurement by instruments of the original habitat and the new one, (2) the experiment itself and (3) the measurement of results, *i. e.*, the determination of the degree of morphologic and histologic difference. The detailed procedure in each of these has been given in "Research Methods in Ecology"[1] and it is unnecessary to repeat it here. It is sufficient to indicate that experiment should proceed whenever possible

[1] Research Methods in Ecology, 25, 145.

along three parallel lines, which have been designated as (1) natural experiments, where advantage is taken of natural movement into new habitats, (2) habitat cultures, where reciprocal plantings are made in original and new habitats, and (3) control cultures, where the experiments are carried on in plant-houses, where they can be controlled and directed at will. In addition to this, definite experiments for the determination and production of constancy are of fundamental value. In regard to the evaluation of the new form when once produced, it will suffice here to state that this should be concerned both with the individual and with the group of individuals. The proper determination of the latter is the task of biometry, when it has attained the necessary development.

For the preservation of the results obtained by the ecologic methods briefly sketched above, an *evolution herbarium* is proposed. It is felt that the usual taxonomic herbarium will have its usefulness restricted more and more to the preservation of types, and to the purposes of instruction. The evolution herbarium will be the record of field observations and experimental results. A species or a form will be represented in it by all the variations that can be discovered, and each variation by a large number of individuals. The new forms produced by nature, and by experiment in nature or under control, will likewise be adequately represented. This representation will take the form not only of the usual dried specimen, but of photographs, drawings, slides, preserved material, etc. With all this, however, the evolution herbarium is still to be regarded as a record merely. It is not to replace the taxonomic herbarium as a mass of working material to be shuffled about and made into species. It is a repository of species and forms when they have finally been determined by experiment.

IV. Nomenclature and Treatment of New Forms

Enough has been said to indicate clearly the ecologist's view of species, both valid and otherwise. He is vitally interested in the species' ancestry, its method of origin and the factor concerned, as well as in the result, which is the species or form itself. Until his experimental study of these points makes it possible to distinguish species from minor groups, or shows that the species concept is a mistaken one, it is useless to debate whether the resulting form is a species or not. In fact, the status of the result must await the determination of ancestry and origin in every case, and we may well call all the results forms until this has been done for each.

The question of ancestry resolves itself at the outset into one of old forms or of forms newly produced. The production of a new form from an old or existing one by properly checked experiment at once gives the ancestry of the former. Here, where the whole experiment is under our control from beginning to end, we may concentrate our attention upon the method of origin and the factor concerned. The discovery of the ancestor of an existing form or species is often a much more difficult matter. Until the ancestry is determined, it is useless to try to ascertain the method of origin, and the factor. When the form bears the distinct stamp of sun or shade, of a wet or dry habitat, or of hybridation, etc., our search is narrowed at once to deciding what species gives the most promise of being the parent form. When there is no distinct stamp, we must first look for the most promising species, and then try the various methods and factors experimentally until the form sought is produced. How often the ancestry and origin of accepted species can be worked out in this way remains to be seen. Results already obtained show that this method works perfectly in the few cases tried, and that it may be expected to prove successful in many cases. When a complete series of trials of suspected parents does not give the form sought, it seems fair to assume that these and the species

sought are more or less coordinate. In this process, it is probable also that light will be thrown on the question of their derivation from a common stock or from two or more stocks.

The four methods by which new forms originate have been discussed before this society in a paper read last year. These have also been given in some detail in print[2] and are so generally well known to botanists that detailed consideration of them is unnecessary here. These four methods are adaptation, mutation, variation and hybridation. Variation alone has not yet been certainly established by experiment as a method by which new forms originate, but the evidence of it is so strong that it amounts to presumptive proof. It seems certain that for plants at least it is not the principal method, as Darwin thought, and that it is probably much less important than adaptation, and probably also less important than mutation. It is, however, a much more obscure process, and it is impossible to tell in the absence of any critical experiments just what it is, or what its importance may be. Darwin has said: "I have spoken of variations sometimes as if they were due to chance. This is a wholly incorrect expression. It merely serves to acknowledge plainly our ignorance of the cause of each particular variation." The exact measurement of habitats has made it clear that minute variation in the factors of the habitat is a very important if not the ruling cause in the production of minute variations in structure. In the case of the minute initial variations shown by the individuals of a group, it is impossible to tell at present how much is due to heredity and how much to causal variation of the habitat. It seems probable that the former may control in some forms, and the latter in others. Furthermore, while hybridation stands apart sharply from the others as a process in which existing characters are mixed in some degree, it is becoming more and more probable that adaptation, variation and muta-

[2] Research Methods in Ecology, 147; Plant Physiology and Ecology, 185.

tion are only different phases, perhaps merely differences in degree, of the fundamental struggle between heredity and environment.

Forms arising by adaptation have been called *ecads*, those from variation, *variants*, and those from mutation, *mutants*. With the familiar term *hybrid* for the product of hybridation, we are able to designate in a general way the forms originating by the four methods. The ecologist, and sooner or later the whole botanical world, must have some definite way of naming each particular form. It is possible to take no further thought about the matter, and allow this nomenclature to grow in the same random, unscientific fashion that nomenclature has always grown. It seems highly desirable, however, to consider the requirements of the case, and make suggestions as to the best method of meeting them. The first essentials of a name are that it should be as short and as significant as possible. For our present purpose, the name of each form should indicate the ancestry and the method of origin, and, when it is known, the causal factor. Many ways of securing this result have been considered for each method of origin. This may be illustrated by the following list, showing several possible ways of naming the shade ecad of *Galium boreale*.

1. *Galium dubiosum* n. sp.
2. *Galium boreale dubiosum*.
3. *Galium boreale*.[2]
4. *Galium borealades*.
5. *Galium boreale scias*.

The first method, which is that of descriptive botany at present, indicates nothing of ancestry, origin or factor. The second gives merely the ancestry, as does the third. The fourth gives both ancestry and method of origin, the patronymic suffix *-ades* referring to ecad. The use of a suffix has much to commend it, particularly the fact that it makes it possible to designate the forms of a species by means of a binomial. Its use, however, has practically been made impossible by the senseless names

that have too often been given species. The fifth method, though requiring the use of the trinomial, is the best. It has all the brevity possible, and yet indicates ancestor, method of origin and factor concerned. It is interesting to note that this problem was worked out in 1902 in essentially the same fashion.[3] The shade form of *Galium boreale* was then called *Galium boreale hylocolum.* The present method has the advantage of brevity, and of referring directly to the causal factor concerned in producing the ecad rather than to the habitat as a whole. It is a relatively simple matter to recognize and produce sun and shade ecads, wet and dry ecads, but ecologic analysis can hardly go further at present. Consequently, the use of *scias, helias, xeras* and *hydras,* denoting respectively shade form, sun form, dry form and wet form, will not only enable us to designate all new ecads briefly and conveniently, but it will also reveal the ancestor, method of origin and causal factor at a glance.

After much puzzling, it seems that it will prove difficult, if not impossible to improve upon the conventional method of designating hybrids, viz., *Galium boreale* × *trifidum.* Until more is known of variants, it is proposed to designate them by a brief and applicable trinomial term, *e. g., Galium boreale exiguum.* While this is the usual trinomial, it would at once reveal the method of origin, as well as the ancestor, by virtue of the fact that the other three methods of origin have their proper trinomial form. In our present knowledge of mutants, it seems impossible to take the cause into account. The suggestion is accordingly made that the mutant be named with reference to its most striking characteristic, the trinomial term to bear the prefix *per,* very, referring to the saltatory nature of mutation, and thus denoting the method of origin. The value of these suggestions may be indicated by comparing the trinomials thus formed with the corresponding binomials.

[3] Herbaria Formationum Coloradensium.

Cerastium oreophilum = *Cerastium strictum scias:* ecad.
Verbena intermedia = *Verbena stricta* × *hastata:* hybrid.
Aquilegia jamesii = *Aquilegia cœrulea peralba:* mutant.
Machæranthera aspera = *Machæranthera viscosa aspera:* variant.

In concluding, the ecologist will confess frankly that he does not know what a species is. On the other hand, he is certain that he knows some of the things it is not, and that the species of the descriptive botanist comprise several widely different things. Just what these are and what their relation to species, if there are such, is a matter to be decided by experiment alone. The question of what a species is can not even be answered provisionally until a sufficiently large number of experiments have been made to indicate the regular procedure in the origin of plant forms and to reveal the principles that control it.

AN ECOLOGICAL ASPECT OF THE CONCEPTION OF SPECIES

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In the discussion of this question I do not feel myself hedged in by any limitations, since no one pretends to say what are the bounds of ecology. Indeed, to define a species may be regarded as an easy task, compared with the task of one who sets out to define ecology. And so this occasion affords me a pleasant opportunity to present some views for which I have long desired an audience like this.

It is coming to be realized that the problems of physiology and ecology are essentially identical, not alone in the matter of the species concept, but in all respects. Physiologists and ecologists have come to feel that the experimental method furnishes the only adequate test for determining the validity of species. The method of approach has differed with the point of view, and it is the physiologist who has given most emphasis to the fundamental importance of experimentation. The ecologist, on the other hand, has brought in the rich contributions of field observation. It is only recently that each has recognized the imperative necessity of the method of the other, and it now seems possible to predict that the fundamental method of the future is to be field experimentation combined with observation. No one realizes so well as does the ecologist the inadequacy of laboratory experimentation in the settlement of field problems. The ecologist feels that the species problem is essentially a field problem, and hence incapable of final settlement, either in the herbarium or in the laboratory. Yet it is the exact methods of the laboratory carried into the

field that give promise of the solution of the problem of species.

Perhaps no phenomena bring the principles just enunciated into more clear relief than do those of natural selection. Many species must be born that never have an opportunity to survive, owing to their lack of adaptation to the surroundings in which they originate. The mutants of *Œnothera lamarckiana,* though developed under essentially similar conditions, do not appear equally adapted to the environment in which they first appeared; had they been left to themselves, some mutants would have perished, while others (and perhaps especially *Œnothera gigas*) might have lived. The citrus hybrids, developed in government experiments in Florida, form another group of new forms, some of which are best adapted to one climate, and others to another. Since, therefore, no necessary adaptive relation must exist between a new species and the region of its birth, it is clear that the laws of selection determine the success or failure of new species. The interpretation of selection is a field problem, an ecological problem. A theoretical plant species may be produced in the laboratory, but the real species that make up the vegetation of the world are developed and must be studied out of doors.

One of the noblest aims of ecology is the destruction of many of the "species" of our manuals. Where the critical study of species is confined to the herbarium, it often happens that ecological varieties or habitat forms are given specific rank. An excellent instance of this is seen in the case of *Polygonum amphibium* and *P. hartwrightii.* The latter, which looks wonderfully different from the former in herbaria, can be developed at will by growing *P. amphibium* on land instead of in the water. Not infrequently a plant may be found on the edge of a pond, showing branches in the water that would commonly be referred to *P. amphibium,* and aerial branches that would be regarded as *P. hartwrightii.* Bonnier's classic experiments, whereby many alpine

plants were shown to be capable of being developed into well-known lowland species in a single generation, illustrate a phenomenon similar to that exhibited by Polygonum. It is likely that our manuals contain many so-called species, such as these, which await reference to ecological varieties.

Having eliminated habitat forms from the rank of species, and having disposed of the influence of natural selection as a destroyer of many incipient species, it remains to discuss the varied ideas concerning the real or supposed species that remain. In the main it may be said that there are two opposing conceptions of species that are to-day struggling for mastery in the realm of biologic thought. The more prevalent idea, dating in its essence from the time of Darwin, has been that species are artificial creations, mere matters of convenience in the classification of the organic world, arbitrary concepts that have no great and enduring reality. Partisans of this view hold to the doctrine of continuity, maintaining that all species have been connected with other species by a series of intergrades, and that there is no vital distinction between variation and mutation. If, indeed, many species, such as the sassafras, differ widely from all other known species, this is because of the elimination of intergrading forms. In the case of Sassafras, this idea is strengthened by the evidence furnished by fossil forms. In somewhat striking contrast to this concept of species stands the idea that species are entities, which arise by discontinuous variation or mutation, and which have their full specific value from the start. Nor does time change specific form by any slow gradations; the species at its death shows no essential difference from the species at its birth. In many instances, at least, these species are of lower rank than the Linnean species, and have been known as small or elementary species. As a rule those who hold to the latter species conception are more prone to appeal to hidden "internal" causes in explaining the origin of new species, while environmental

factors in evolution are more commonly held as dominant by those who regard species as indefinite things gradually evolved from other species. In this connection it is curious to note that the idea of a species as an entity, now held by most mutationists, has much in common with pre-Darwinian notions of special creation; it seems to be in part a return to former conceptions of a rigid nature. On the other hand a new idea of species content is set up. Both pre-Darwinians and Darwinians agreed that *Draba verna* is a species, but the new school would maintain that under this name are masquerading a hundred odd real species.

There are, then, two radically different conceptions of species now current, one of a rank as much higher than the other as the genus is above the Linnean species, or the family above the genus. Ecological observations support both views, but it is especially the experimental method that has made things clear. Whether or not one calls them species, it is evident that the genus Œnothera contains a number of entities, sharply defined from one another. In such genera as Salix and Aster there is reason to believe that species do not thus differ sharply, but that they are connected with one another by all but imperceptible gradations; at any rate this condition exists in Leptinotarsa, as conclusively shown by Tower. It seems impossible to homologize species in Œnothera and Leptinotarsa. It appears that the method of evolution in various groups of plants and animals is radically different, and it follows as a corollary that what are called species in these various groups are necessarily not homologous.

In the light of these views the task of the taxonomist is seen to be most difficult; for the convenience of biologists, he must reduce to common terms things that are unrelated; he must homologize things that are not homologous. In such a dilemma there seem two courses open: (1) The Linnean species concept, that has ruled both before and after evolution was accepted by biologists,

may be abandoned. The elementary species then becomes the species of taxonomy. Something akin to this has already taken place in certain genera, notably Cratægus, Viola and Sisyrinchium. Those who take this attitude should abandon the year 1753 as a starting point for specific nomenclature, since a new conception of species demands a new datum line. Possibly this datum line is furnished by the experimental work of Jordan on *Draba verna.* Such a revolution would of course be appalling in its consequences. The present status of Cratægus, perhaps, gives an index of what is to come, if this idea is accepted; where now we have dozens of species, we may expect hundreds or even thousands. We may even expect the appearance of a taxonomic daily newspaper with its hourly record of new species and their fluctuations, comparable with market quotations in a period of financial panic. (2) The alternative is to retain the Linnean species concept as a working theory, employing trinomials for elementary species. Thus we should speak of *Œnothera lamarckiana rubrinervis, O. lamarckiana gigas,* etc. One great advantage of following this method would be that we should secure all the advantages of the newer critical study of such genera as Cratægus and Sisyrinchium, and at the same time tie the new work to the old in such a way that those not taxonomists could appreciate the general significance of the results. Very few except Cratægus specialists could tell offhand anything about *Cratægus ellwangeriana* or *C. champlainensis,* but if these forms were denominated respectively, *C. mollis ellwangeriana,* and *C. mollis champlainensis,* many would know their general affinities, In the case of intergrading species without well-defined specific boundaries, the only course is to retain the trinomial for varieties, much as has been done in the past. If it is wished to distinguish between varieties and elementary species, the expression var. might precede the varietal name, as is the custom now with many.

It is to be hoped that the taxonomists, and particularly

those taxonomists who have sinned in the much making of species and those who have made a so-called critical study of plants without any adequate training in the general principles of botany, will reform their ways. In truth, they must reform. No longer may each man be a law unto himself. Nor is it right that any group or coterie should make rules and regulations that run counter to the expressed opinions of a world botanical congress. It is doubtful if any single botanist agrees with all of the taxonomic expressions of the Vienna Congress; it is even possible that some agree with none of its provisions. However, it registers a general consensus of opinion, agreed upon by those who thought the congress far too radical, and by those who thought it far too conservative. It marks a step in the taxonomic progress of the botanical world, and there is no surer way to lead toward further progress than in abiding by its provisions; on the other hand, there is no surer way of ensuring the continuation of the taxonomic chaos, of which we have had far too much, than in setting up individual or even provincial or national codes in opposition to a world code. An American school of taxonomy is an anomaly, since many species are world-wide, and should have world-wide names; even the local species should be delimited in accordance with international rules.

Taxonomy must be scientific. It must require for its devotees a training as rigid as that required by professional workers in morphology, physiology or ecology. Species-making by taxonomic tyros must be abandoned. The requirement of Latin diagnoses, though regretted by many of us, may be of help in checking the voluminous contributions of amateurs. In the future it must be recognized that the final test of the validity of species is experimental, and taxonomists must work no less in the herbarium, but more in the field and in the garden. If the taxonomists of the future fail in these respects, a hard but certain fate awaits them. The world of

morphologists, physiologists and ecologists has borne with them patiently and long, and has deferentially abided by the specific determinations of the taxonomists. The recent ebullitions of the taxonomic radicals have evoked in botanists in general successively dissatisfaction, contempt and rage. These things will not be endured much longer; a little more and the sinning taxonomists will be "cast out into the outer darkness where there shall be wailing and gnashing of teeth."

DISCUSSION OF THE SPECIES QUESTION.

At the close of Mr. Cowles's paper the chairman invited those present to discuss the question. The following remarks were made:

Mr. J. M. Coulter: I find myself in some particulars agreeing with every speaker, and it seems to me that there are enough elements in common in all that has been said to enable us to reach some sort of working basis. One thing agreed upon in all that has been said is that nature makes individuals and men make species. This means that in a certain large sense the individual is the unit to be recognized. At the same time it is evident that the attempt to record such units on the basis of any present scheme is entirely out of the question. While it is clear that we are approaching greater uniformity in our conception of species, we shall not reach agreement until we know more definitely the influence of ecological and physiological factors, if we may separate them for the moment, upon structures. But until this knowledge becomes more exact, how shall records be made? We must have some temporary and effective method. We all appear to recognize the fact that the indefinite multiplication of names of species must be stopped sooner or later, and the sooner the better; for we are getting the record into a condition that makes it unworkable. It seems to be the belief of every speaker that something must be done, and that the conception of a species must be modified eventually. It is quite evident that we are in no position as yet to formulate definitely what we shall agree to call a species, and in the meantime it seems to me the suggestion made by Dr. Britton is a very workable one. It gives to every one the opportunity to distinguish and record forms clear down to individuals if he chooses; and at the same time

it removes the grievous burden of a great multiplication of names. It seems to me that the suggestions of Dr. Bessey and Dr. Britton almost meet at this point. In effect, it means to continue to name easily recognized forms, calling them species if desired; and then by a system of numbers to indicate the more refined distinctions. This avoids the great multiplication of names and secures an exact record. This method has been developed so effectively in the cataloguing of stars and books that it could be adapted for plants without serious trouble. I would ask Dr. Britton how much this scheme would reduce the number of published names.

Mr. N. L. Britton: I do not know. Those that have been published up to this time it would reduce probably two thirds.

Mr. J. M. Coulter: A reduction of the names to one third would be a good start, and I think we had better hold Dr. Britton to his idea. I think we can get together on this suggestion, so that all botanists can recognize the ordinary forms and remember their names, and the taxonomists can record the more refined distinctions. I had not heard of this proposition before, but at present it appears to me to be desirable and workable.

Mr. J. B. Pollock: I should like to say a word along the line of work upon which Dr. Arthur has presented some thoughts to you, but I think we can go a little further than Dr. Arthur did in his argument in regard to a definite method of getting at species from the physiological basis, and the people who are nearly ready to begin that, I feel sure, are those who have worked with the fungi from the cultural side. In talking with a number of men, who are interested in that side of the work, in the course of these meetings, I have been impressed with a fact the importance of which has been growing upon me in my work alone, that the men who are doing that kind of work are feeling the absolute necessity of doing something definite exactly along the line which has been indicated by almost all the speakers here in a general

way. Now, what I mean is the kind of work which was reported in the botanical session this morning on Penicillium and its relation to definite culture media, and I believe in the very near future we shall be describing species, of many of these fungi in a definite relation to culture media. A species will be a group of those organisms which show a certain combination of morphological characters when grown upon a medium of definite and known composition. The type of the species involves a type medium, and the fluctuating variations must be determined by the use of a series of such media. Considerable work in this direction has been done, but the method has not yet been well adapted to taxonomic description. I think we are ready now to do this work from a strictly taxonomic point of view. That will be doing exactly what at least four of the speakers have advocated, but they did not tell us in detail how to do it. These fungi are particularly suited to this kind of work for several reasons. In the first place, they are small in size and we do not need a garden in which to grow them; we can grow them in a test-tube. In the second place, they reproduce exceedingly rapidly and we do not have to wait a year or ten years in order to get them to produce new generations. They may do that in a few hours, or at most in a few days, so that we can produce generation after generation, while the man who is working with flowering plants is waiting for one generation to develop. Hence these plants are favorable material with which to begin the kind of work which seems to be demanded, namely, the union of the morphological and physiological factors in the description and delimitation of species.

Mr. T. J. Burrill: I do not know that I have anything very definite to say, but I am somewhat conscious of a feeling that I am glad that I am not a taxonomist this afternoon. The taxonomist has certainly suffered this half day. It was said here a few moments ago that there had been no progress along the line of the systematist;

that we have developed greatly elsewhere, but in this particular we have remained medieval or worse than that. I think we have abundant evidence right here that there has been progress. This meeting this afternoon would have been no more possible a dozen years ago than it is now to separate out the species of Cratægus by somebody who has not studied them during that time. There has been something working. People have been finding that there is something besides names and dates; something has occurred since 1753. It looks to me as though it were hopeful. If there is anarchy, more of that than anything else, it is a pretty good beginning to start something that is not anarchy.

However, I feel sure I shall not give up everything in regard to our common notion of species and species' names. I do hope that I shall know the white oak under its proper name hereafter when I see it, and a few other things like that; and I think it is really important that when we speak about certain things, of certain effects and relations, we do understand what we are talking about and that others may also understand. I think it does make a difference as to whether we continue the use—to take Dr. Arthur's first illustration—the definite use of such terms as *Bacillus anthracis* and *Bacillus typhosus,* and the rest of them. If a writer is going to discuss a subject in which these organisms play a part and one that is vital to our existence and welfare, it is surely desirable that we should have a correct interpretation of what he means when he uses these terms. I believe we are pretty near that meaning in regard to the common organisms in the group of bacteria, so that we know pretty well what is meant when such names as those above are mentioned, though nobody will deny that included among the organisms to which the names apply there are considerable differences. They are different in their sizes, if you come down to microbe measurements; they differ certainly in their growth upon different media, and I do not see why the physiological

effects may not just as well enter into the species idea as the morphological characteristics, if we can get them; but I do not know how we are going to get them for such plants as forest trees. In the case of the white oak, we have got to take the morphological characteristics alone, so far as I see. We can not plant the seeds and witness the trees as they develop in their various stages until they produce seed again. But in case of the lower forms with a generation a day, we can certainly do that, and I think we ought to do it for specific characteristics.

Let me say, what I am most interested in is that we shall know some things yet by some very well known names.

Mr. E. G. Hill: As we have had considerable talk from the pulpit, perhaps a little experience from the pew in regard to species might be of use. In 1874, I came to that part of Illinois which is now embraced in the city of Chicago, and the year after I began the study of the flora of the region, the sand region (it was all sand then), particularly this dune region east of the city, and there has not been a year since that I have not been out there more or less. Now, I have not been over every foot of it, but with regard to this plant, the *Polygonum amphibium* that has been cited, I always until about 1890 or 1895, I can not give the exact year, I always saw *Polygonum amphibium,* I never saw the other kind. At that time I noticed this hairy plant, with shorter internodes, growing on dryer places. The exigencies of the expanding city and manufactures outside of it led to the partial drainage or entire drainage of considerable areas of our dune flora. The underground parts of *Polygonum amphibium* are pretty extensive. I never satisfy myself without digging up the entire under part of plants, or digging up the root—I can follow a root ten feet, if necessary. When those wet places were drained, the roots persisted in the sand, and the plants while preserving their full form when in the water, would be hairy, and you can trace them all the way from the water up,

may-be twenty to thirty feet from the edge of the water, making their way even along paths or roads. Now, I want to say, I do not know that they did not exist before that, but I never noticed them until then; and not a mile or two miles from here, if there are vacant lots, you will probably find *Polygonum hartwrightii* in a drained slough, where twenty to twenty-five years ago you would not find anything of that kind, but you would find *Polygonum amphibium.* It seems to me that is the way in which it might have originated here. This experience extends from about 1875, and although I gather from it that it was not here before, I believe that it made its appearance not far from 1890 to 1895.

Mr. G. H. Shull: In one sense the recent discoveries in the realm of variation and heredity appear to lead to a backward step in the concept of a species, since the view of the naturalness of species to which these discoveries lead, resembles the earlier view. Upon a comparison of the basis of this conception, however, in the time of Linnæus, with the present situation, the contrast becomes sufficiently striking.

At that time no cognizance was taken of the importance of variations. When variations were first fully taken into account, about the middle of the last century, they were apparently conceived to have no natural limits, and in consequence, no form-group could have natural limits.

The demonstration that variations have natural limits has shown that the lowest grade of form-group is a *natural* group of individuals differing from each other only by fluctuations. It appears to me that the able discussions to which we have listened might all be reduced to the question of the desirability or feasibility of looking upon these *ultimate, natural form-groups as species.* This question largely rests upon the question of utility, and herein lies our difficulty in reaching a universally satisfactory conception. To the maker and keeper of herbaria and to the field naturalist, utility requires that species shall be separable by characters which may be

recognized by a more or less careful examination of a single individual of unknown ancestry. To the experimentalist, whether he be a physiologist, an experimental morphologist or a pedigree culturist, such a conception of species makes them of no utility, and this is also largely true with students of cytology, anatomy, etc., who study the morphology of structures not externally visible. As a student of variation and heredity from the experimental side, I hold that the *natural* group is the only one that can be of any utility to any one but the herborizer, but I do not insist on the privilege of calling this natural group a species. That matter is entirely immaterial. To avoid confusion, we are now calling these groups elementary forms, but this expression is unnecessarily cumbersome for the constant use the conception must have in the future literature of botany, and I hope that some one will come forward with an acceptable short designation for these, in case the herborizer succeeds in checking the trend of development of the conception of species from an arbitrary to a natural one.

Experimental evidence at the present time shows at least two grades of form-groups. These were recognized by Dr. De Vries under the names, elementary species and varieties. By "varieties" De Vries indicates those forms which differ from their nearest related form in one or more characteristics, which behave according to Mendel's law upon crossing with it. As taxonomists have definitely abandoned the use of the term "variety" to the horticulturist, we need a new word with which to speak of this very definite class of forms. As we have taken liberties with the name of Mendel in the formation not only of the adjective "Mendelian," but also the verb "Mendelize," there seems to be no reason why we might not go farther and call these Mendelian varieties Mendelities. These Mendelities are hangers-on of species, and corresponding Mendelities may belong to many different species, as may be illustrated by the frequency of occurrence of white-flowered or albino forms, which differ

from their corresponding pigmented forms in no other character but that of pigmentation. Whether Mendelities may in any case be the initial modification leading to new elementary species is not known, but I believe that we are not yet warranted in so considering it. But elementary species and Mendelities are certainly natural entities and must be used as the physiological units of form.

Mr. J. A. Harris: It seems to me that while the systematists are receiving the congratulations of morphologists and ecologists, it will be well for us to remember that he "that is without sin" among us "should cast the first stone." I think in the present state of biology, the morphologist and physiologist and ecologist have some points to learn from the systematist, and that the morphologist, physiologist and ecologist are to some extent responsible for our present inadequate knowledge of species.

The taxonomist has worked out a very careful scheme of recording his observations; he feels himself bound, in preparing a monograph, to cite all descriptions. It is perfectly easy to take a well-prepared monograph and to follow out the earlier literature of any form. If, on the other hand, one turns to morphological and physiological writing, he will find it is a difficult task to locate the work which others have done on the same species. It seems to me that if the taxonomist is expected to make use of experimental and ecological data in his limitation of species, he should be given the data, by those who are doing such work, in a form in which he can use them. Take, for instance, our ecological papers. An ecologist works on a certain region and refers to a number of species definitely, and to a larger number of species indefinitely, grouping them as grasses, sedges, asters, etc. How is the taxonomist to utilize such data. The work of the ecologist should be specific and comparative. He should be explicit in his statements concerning the form and life conditions of a species in his own region, and he should refer to the literature in such a detailed fashion

as will enable the systematist to determine the characteristics and the environment of the same species in another region. I think the morphologist, too, must adopt the practise which the systematist has found indispensable. He should cite in a clear but condensed form all the pertinent morphological literature for each of the species which he treats. The recognition of this obligation would, I believe, do much to raise the standard of our published work, and it would place at the disposal of the systematist a mass of data which he ought to use to great advantage.

Mr. A. E. Hitchcock: I wish to call the attention of the ecologists to one very important method by which they may greatly aid the taxonomists. The former are doing much careful work in studying the ecological relationships of plants, but in order that this work may be checked up and be available to taxonomists it is necessary that specimens of the species studied should be prepared and deposited in a public herbarium. Unless such a permanent record can be made the statements concerning habitat, variation and other ecological data are of little value to the systematist, because they can not be verified. Such verification is especially necessary because the ecologist is not likely to be sufficiently familiar with all groups of plants to pass authoritatively upon their botanical names. Even when the plants are submitted to taxonomists for identification it may happen that errors occur. Data based upon specimens available in public herbaria would aid ecologists themselves to coordinate their work. Taxonomists will be glad to avail themselves of all serious work done by ecologists when the data can be definitely connected with preserved specimens.

One other point. I wish to emphasize the necessity of field work in determining the limits of species. If possible, taxonomists who are monographing groups of plants should study these plants in the field. The botanist can determine usually to his own satisfaction the limits of variation of a single species in a given

locality. The herbarium then becomes a record of his field observations. Much good work can be done in the herbarium, but when coordinated by abundant observations upon the plants, as they occur in nature, the conclusions are much more likely to be correct.

Mr. G. H. Shull: I would like to say one word in reply to Mr. Hitchcock's remarks regarding what we know about variations when we seen them in the field. It is my experience in the cultivation of things brought in from the field during the last four years, that we know nothing about the significance of variations in the field as to their bearing upon the question of the species, if by species we mean a continuously variable group, because in some instances we find that very distinct variations as seen in the field are immediately lost when the individuals possessing them are grown under uniform conditions. We find, on the other hand, that equally distinct, or even less distinct variations—as determined entirely by an estimate of the difference in form—are retained with absolute permanence so far as one can determine by three or four years of culture under like conditions. Now, how we can tell without an experimental basis for the estimation of the meaning of variation in any particular species, what is the significance of those variations as we see them in the field, I am at a loss to understand.

SHORTER ARTICLES AND CORRESPONDENCE

OTTER SHEEP

THE following account of the "otter" sheep occurs in Vol. III, p. 134, of President Timothy Dwight's Travels in New England and New York; New Haven, 1822. It is more explicit than any I have seen before, and may be of interest to naturalists. The date of the journey in which this account appears was about 1798.

Mendon, the township mentioned, is in Massachusetts, about eighteen miles southeast of Worcester.

"In this township, if I have been correctly informed, an ewe, belonging to one of the farmers, had twins, which he observed to differ in their structure from any other sheep in this part of the country; particularly the fore legs were much shorter, and were bent inward, so as distantly to resemble what are called club feet. Their bodies were, at the same time, thicker, and more clumsy. During their growth they were observed to be more gentle, less active, less inclined to wander than other sheep, and unable to climb the stone walls with which this region abounds. They were of different sexes. The proprietor, therefore, determined on an attempt to produce a breed of the same kind. The attempt was successful. The progeny had all the characteristics of the parents, and although they have since multiplied to many thousands have exhibited no material variation. I am further informed that the breed has been crossed with a breed of sheep common in this country; and in all instances to the date of my last information, the lambs have entirely resembled either the sire or the dam; and have never exhibited the least discernible mixture.

"These sheep are called the Otter breed from a resemblance to the animal of that name. Their flesh is said to be good mutton; and their wool not inferior to that of common sheep, either in quantity, length, or fineness. But their peculiar value consists in the quietness with which they continue in any enclosure. In a country where stone walls are so general as in many parts of New England, it would seem that sheep of this description must be almost invaluable."

C. L. BRISTOL.

NEW YORK UNIVERSITY,
March 18, 1908.

NOTES AND LITERATURE

EXPERIMENTAL ZOOLOGY

Przibram's Experimental Zoology, of which Part I has just appeared,[1] is an enlargement of his brochure of 1904. It is the author's purpose to publish four other parts dealing respectively with Regeneration, Phylogeny, Vitality and Function.

The present volume brings together the modern experimental work dealing with the egg and embryo. The results are grouped under the headings of Fertilization, Egg-structure, Karyokinesis, Gastrulation, Developmental Mechanics and Influence of Environment. There is a very full bibliography, and sixteen partly colored plates. These plates contain many figures familiar to the student of modern literature of the subject. The figures are often too small and their arrangement in plates at the end of the book is not as advantageous as figures at suitable places in the text would be, nor would their simple character preclude their insertion as text figures.

The book will prove most useful, giving as it does a very complete résumé of the subject. The matter is treated in large part as a series of reviews under topic-headings of the results obtained by each author, and in the present state of the subject no other method is perhaps feasible; but while this treatment is satisfactory as a résumé of what has been done, it is not an arrangement that furnishes entertaining reading to the uninitiated.

At the end of each chapter the author attempts to draw general conclusions from the evidence reviewed, and inasmuch as these conclusions serve to register the author's point of view we may examine them in some detail.

The work of recent years on artificial parthenogenesis leads to the conclusion, in the author's opinion, that the cause that calls forth the further development of the quiescent egg-cell is to be found in the hastening of the vital processes already existing in the egg by means of the withdrawal of water from the

[1] Experimental Zoologie. Part I, Embryogenese. By Hans Przibram. Franz Deuticke, Leipzig, 1907.

egg. Normal fertilization is supposed to act in the same way. The evidence at hand does not appear to the reviewer to substantiate this generalization, because the shrinkage sometimes observed in the normal egg may be an effect of changes taking place rather than their cause, and because, in the second place, some of the most recent results, especially those with weak acids (Lefevre), can scarcely be interpreted on Przibram's view. There are some indications, on the contrary, that fertilization is a vital act in the sense that the sperm is a stimulus starting development in the same way that many external agents call forth the nerve impulse in a nerve. Here also in the nerve the same impulse may be called forth either by internal factors or by external agents. The intimate nature of irritability of living material remains, however, as much of a puzzle to the physiologist as to the embryologist.

The occurrence of visible inclusions in the egg,—pigment, yolk, granules, etc.,—leads the author to conclude that even before fertilization the egg is made up of different substances, which "guarantee" the subsequent development. We touch here on one of the burning questions of modern embryological speculation, for while certain evidence seems to show that different substances contained in the egg furnish a "guarantee" of diversity, still the central problem remains untouched, for few, if any, experimentalists will admit unreservedly that these materials are preformed primordia, or organ-forming substances in a strict sense, rather than that their presence is a condition that prejudices in certain directions the subsequent development. In other words we are still unable to state how far and in what sense the development is due to preformed materials and how far it is an epigenetic phenomenon depending on the relation of the parts to each other in a dynamic sense. It may be well in the present unsettled state of the subject not to prejudice these questions, for, there may be truth on both sides, since predetermination and epigenesis are not mutually exclusive possibilities, but rather complementary.

In regard to the location of the first cleavage plane, Przibram points out that this is "given" by the location of the segmentation spindle. The position of the spindle itself is the result of the egg structure, the geometrical form of the egg and the meridian of fertilization. The position of the spindle in any particular case may be due to any one or to more than one of these factors. The causal problems still remain to be considered.

The division of the centrosomes, the formation of the astrosphaeres, the division of the chromosomes and of the cytoplasm, are not to be considered, according to Przibram's summing up, as constituting a series of causally connected events, but are the result of the same primary cause. While this point of view is sympathetic to the reviewer also, it should be clearly understood that we entirely lack sufficient evidence to establish such an attractive interpretation. Even if all these changes are the result of one cause, we can form no conception of what that cause may be. Our author's conclusion, at the end of the next chapter, to the effect that this common cause is to be found in a system of surface tensions, can scarcely be said to be at present more than the working hypothesis of a few thinkers of the school of developmental mechanics. One does not have to look very far for facts that are difficult to explain on such a view.

It is pointed out at the end of chapter VI. that the arrangement of the blastomeres conforms to Plateau's law of minimal surfaces. While it is true that such a law may appear to account for cell arrangement, we should not overlook the fact that a similar arrangement follows if the cells are simply flattened against each other by pressure from outside. Possibly also the mutual flattening—an active process—of the cells themselves might give the same arrangement. Therefore we do not know that surface tension plays even the chief rôle in the result. In fact, the author himself concludes in the next chapter that gastrulation is the outcome of chemotactic action, *i. e.*, of an active wandering of the cells. Such a conclusion appears to admit that the characteristic feature of formative processes may be responsive in its nature rather than chemical or physical.

The chapter dealing with the developmental mechanics of differentiation takes up the extensive literature describing the results of isolation of the blastomeres and of injuries to the egg. A very complete and impartial review is given here. Przibram attempts to interpret the results in the following way. Different chemical stuffs are supposed to be present in different zones of the egg and these lead to the differentiation of the different organs. If parts of the egg are removed and no rearrangement of the formative stuffs occurs, partial development takes place; but if a rearrangement follows, so that the parts recover their normal relations of position, a whole embryo of smaller size results. That the different parts of the egg play the rôle here

assigned to them can not be denied, and this is the simplest interpretation that embryologists have given to their results; but it is improbable that the differences between whole and partial development rest on this condition alone. The phenomena are really more complicated, as shown when whole development occurs even after the materials of the egg have become shut up within cells, and as shown in regeneration when a whole animal of smaller size develops from a part of the body of a fully formed organism.

The final chapter deals with the influence of external factors, and, although compressed into very small compass, most of the modern work is referred to at least briefly. The author's conclusion that external factors play in most cases only a minor rôle in development will be conceded by most students of experimental embryology. Nevertheless, important results have been already obtained from a study of external factors and our causal knowledge of the physiology of development rests in the main on evidence from such studies. Whether the formative changes are simply a complex of physiological relations or depend on factors not usually considered by physiologists is at present a question of opinion rather than of demonstration.

While we have found ourselves obliged in many cases to urge that many of the conclusions reached by the author still remain uncertain, and in other cases to take issue with the author's summaries of the present state of affairs, yet it should be repeated that the chief value of the book lies less in such generalizations than in the conscientious, full and exact review of the literature. The results so far obtained are marshaled forth in excellent order and the book is a valuable storehouse of materials, and will be found useful not only to those who do not have access to the original literature or time to digest it, but also to those who have felt themselves somewhat overwhelmed by the rapid development of this branch of embryology. The general reader, too, will find in this volume a well-balanced summing up of the more important results of the school of experimental embryology.

M.

ICHTHYOLOGY

Jordan on Fishes.[1]—In a single large volume President Jordan presents "virtually all the non-technical material contained in

[1] Fishes. By David Starr Jordan, President of Leland Stanford Junior University. New York, Henry Holt and Company, 1907. Large 8vo, XVI + 789 pp., 18 colored plates and 673 figures. $6.00.

the author's *Guide to the Study of Fishes*. . . . His chief aim has been to make it interesting to nature-lovers and anglers, and instructive to all who open its pages.''

President Jordan can appeal to readers of any age. A delightful account of the ''breeding habits of our smallest sea-horse, prepared by the writer for a book of children's stories'' is found on page 453. In the first chapter the author says that to ''understand a fish we must first go and catch one.'' It is apparently with a boy companion that he starts for the old swimming hole where they catch a sunfish—''a little, flapping, unhappy, living plate of brown and blue and orange, with fins wide-spread and eyes red with rage.'' In describing its life-history, eating is said to be about the only thing a fish cares for. The black swallower engulfs a fish many times larger than itself (Gill); a single goosefish has been found with seven wild ducks in its stomach (Goode); the pike is a mere machine for the assimilation of other organisms; and the bluefish is an animated chopping machine—an unmitigated butcher (Baird). Nevertheless it is fortunate that the fishes can express no opinion as to two-mile seines and some features of the canning industry!

A general description of the structure of fishes, of their habits, adaptations, colors, distribution and economic value, of the mermaid industry and the sea-serpent myths, form the first section of the book—ten chapters.

In the remainder of the book fishes are considered systematically, from Branchiostoma to Malthopsis. In behalf of stability, ''the sole function of the law of priority,'' several familiar and established names have disappeared. Lepisosteus replaces the ''more correct but also more recent spelling, Lepidosteus.'' The general reader, interested in the fishes rather than their names, will find that ichthyological terminology has been made as unobtrusive as possible. Such terms as slippery-dick and pop-eye grenadier make amends for considerable Greek, and common names are freely used.

The reading of this book is not like a visit to a museum, or even to an aquarium; there is more of out-doors about it. In part this is due to quotations from anglers, classic and modern, including Van Dyke's apostrophe to the ouananiche. Chiefly it is due to the author's own experiences and such unexpected comments as—''This is the noted Aweoweo of the Hawaiians which used to come into the bays in myriads at the period of death of

royalty. It is still abundant, even after Hawaiian royalty has passed away." Or—"The coral reefs of the tropics are the centers of fish-life, the cities in fish economy. The fresh waters, the arctic waters, the deep sea and the open sea represent forms of ichthyic back-woods, where change goes on more slowly." Rarely there is a defective or ambiguous sentence, such as—"Turner gives an account of a frozen individual swallowed by a dog which escaped in safety after being thawed out by the heat of the dog's stomach," but the book, as would be expected, is exceptionally well written. It is also well illustrated, and the figures (except Fig. 268) are carefully placed to accompany the text. They include a considerable number of photographs of living fishes, and eighteen colored plates, chiefly of fishes from the coral reefs of Samoa. The volume is attractively printed, except that Chapter XI, The Collection of Fishes, begins with a page on The Classification of Fishes (p. 157); whether the mistake is in omitting the rest of the chapter on classification or in printing its first page is not apparent.

An illustrated description of the changes in the external form of fish eggs during their development, further accounts of nest-building, and the quotation of Brooks' vivid descriptions of the salmon or shad, might perhaps have added to the popular interest in the book. It is, however, sufficiently large, and is full of authoritative information. It accomplishes all that President Jordan planned, and is a comprehensive introduction to a scientific knowledge of fish.

FREDERIC T. LEWIS.

(No. 495 was issued on April 20, 1908.)

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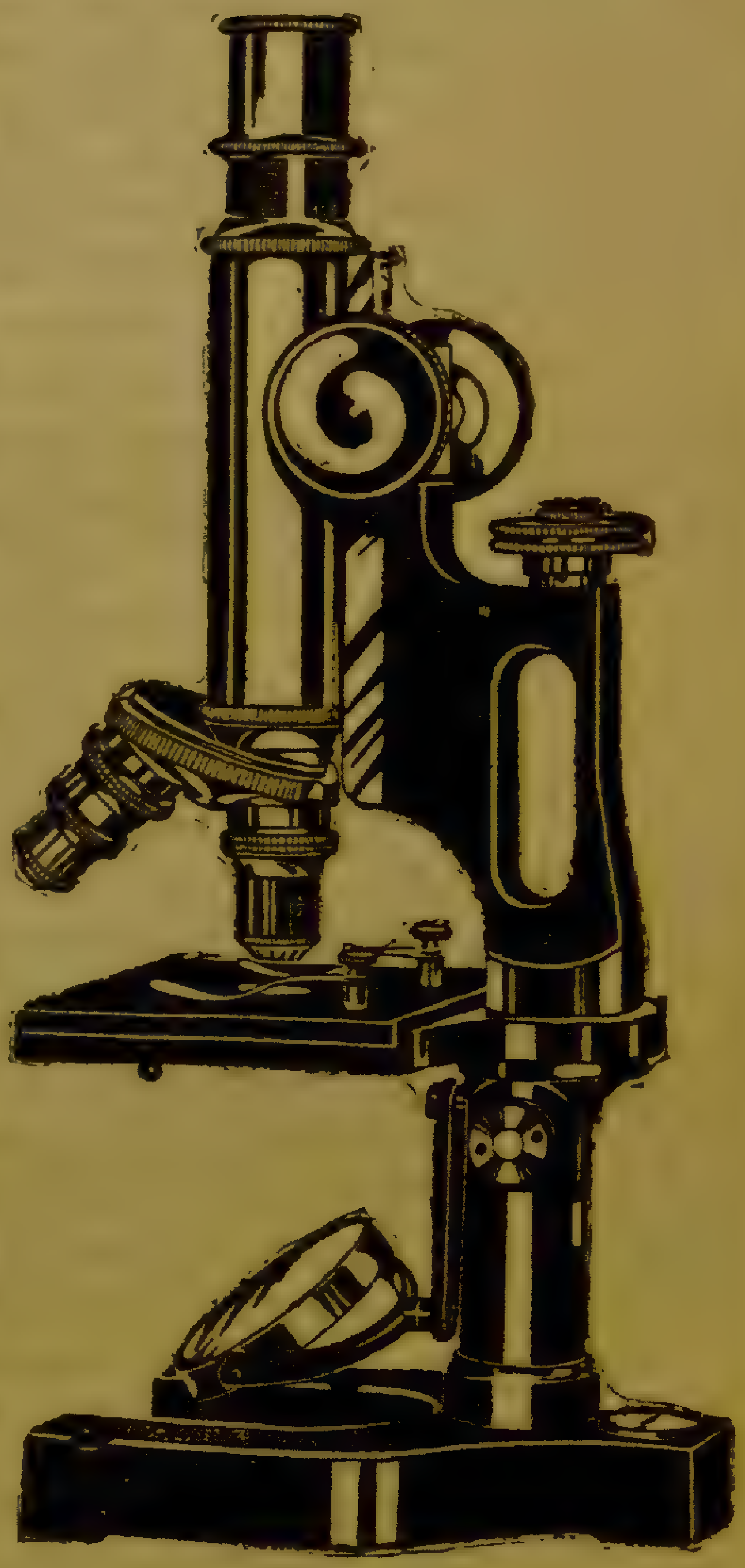

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GLOVER M. ALLEN, *Secretary*

VOL. XLII, NO. 497 MAY, 1908

THE AMERICAN NATURALIST

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IN THEIR WIDEST SENSE

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AMERICAN NATURALIST

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GEOGRAPHICAL DISTRIBUTION; ORIGIN OF THE BERMUDIAN DECAPOD FAUNA

PROFESSOR A. E. VERRILL

Yale University

In a report now in course of publication[1] on this group, 78 species, subspecies or named varieties are discussed, of which 16 have not been previously recorded from Bermuda. Among these, six are described as new.

Of the total number, 72, equal to 93 per cent., have been recorded also from the Florida Keys or the West Indies, or from both, demonstrating the close faunal relations of the two regions. The macruran Decapoda (35 species) show similar relations.

About 53 of the forms (about 68 per cent.) range from Florida to Pernambuco, Brazil, or farther south.

A considerable number, about 25 species, or 31 per cent., extend their range north of Florida to the coast of South Carolina or farther north, the greater portion of these reaching Cape Hatteras. Six or seven reach southern New Jersey.

Two species, *Callinectes sapidus, Eupanopeus Herbstii* and its var. *obesus,* range northward to southern New England, as permanent residents.

Several others occur occasionally or sporadically on this coast, being carried northward by the Gulf Stream, or by shipping, but fail to become naturalized so far north, owing to the cold of winter.

[1] *Trans. Conn. Academy of Sciences,* Vol. XIII, pp. 299–473, plates ix–xxviii.

Fig. 1. *Sesarma Ricordi*, var. *terrestris*, nov. Co-type; × about 2. Phot. A. H. Verrill.

Fig. 2. *Achelous Smithii*, nov.; cotype, dorsal view; × about $1\frac{1}{10}$; 2*b*, chela of the same, front view. Phot. A. H. Verrill.

It is evident, therefore, that the Bermuda decapod crustacean fauna is an offshoot or colony from the West Indian fauna, with only a slight admixture of species from other regions. In this respect the Crustacea agree with the Anthozoa, Mollusca, Echinoderms, etc.

The additions to the fauna of Bermuda, including the new species and varieties, are as follows:

* *Sesarma Ricordi, terrestris,* subsp. nov. See *Science,* Vol. XXVII, p. 491. Fig. 1.
* *Eupanopeus Herbstii, minax,* subsp. nov.
* *Eupanopeus bermudensis,* var. *sculptus,* nov.
Callinectes Danæ Smith.
Callinectes marginatus, larvatus (Ord.).
Achelous Smithii, nov. Fig. 2.
Achelous Gibbesii Stimpson.
Charybdella tumidula (Stimpson).
Mithrax cornutus Saussure.
Challenger Bank, 30 fathoms. Field Museum Nat. Hist., 1905.
Parthenope (*Platylambrus*) *crenulatus* (Saus.). Fig. 5.
Challenger Bank. Bermuda Biological Station, 1903.
Troglocarcinus corallicola, gen. et sp. nov. Fig. 3.
Parasitic in living corals (Mussa, Mæandra).
Dromia erythropus (Edw). Fig. 7.
Argus Bank, 30–40 fathoms. Field Mus.
Dromidia antillensis Stimpson. Fig. 4.
Challenger Bank. Bermuda Biological Station, 1903.
* *Petrolisthes armatus, pallidus.* var. nov.
* *Munida Beanii,* sp. nov.
Argus Bank, 50 fathoms. Field Mus. Nat. History.
Dardanus venosus (M.-Edw.).
Previously recorded under the name of *D. insignis,* which is a distinct species.
* *Clibanarius hebes.* sp. nov.

Those with an asterisk prefixed are known only from Bermuda.

The following 25 species range northward on the American coast to or beyond South Carolina, as permanent residents:

Ocypode arenarius. (To N. Jersey.)
Planes minutus. (To N. Jersey.)
Plagusia depressa.
Portunus Sayi.
Achelous anceps.
A. Gibbesii.
A. spinimanus?

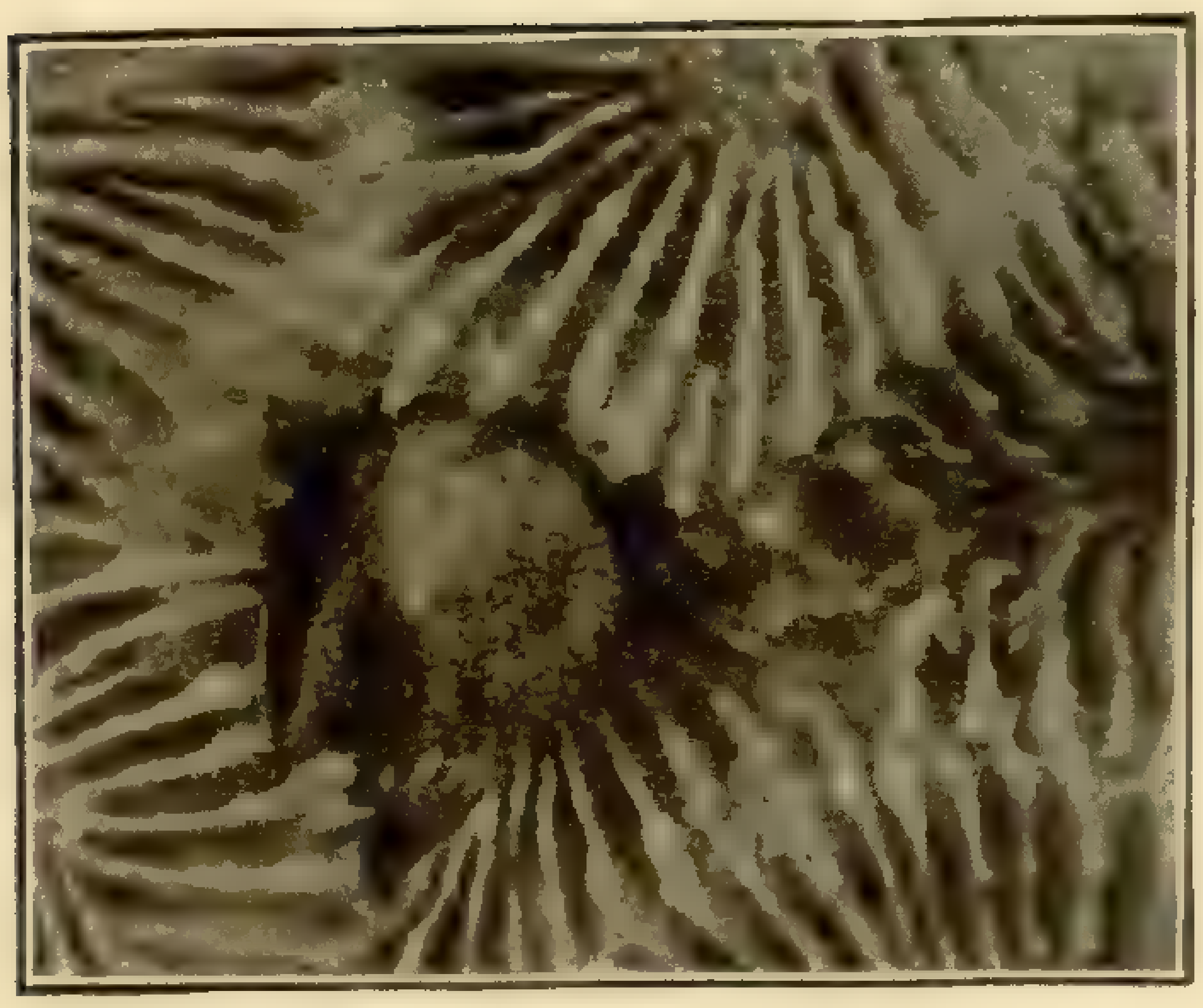

FIG. 3

FIG. 4

FIG. 3. *Troglocarcinus corallicola*, nov., ♀, partially out of its den in a coral (*Mussa*) from Dominica I; × about 2. The crab was intentionally placed in a den belonging to an older individual, otherwise but little of it could be seen. Phot. A. H. Verrill.

FIG. 4. *Dromidia antillensis*; about nat. size. Phot. A. H. Verrill.

Cycyloxanthops denticulatus.
Eupanopeus Herbstii. (To C. Cod.)
E. Herbstii. obesus. (To C. Cod.)
E. occidentalis.
Eurytium limosum. (To N. Jersey.)
Eriphia gonagra.
Callinectes ornatus.
C. sapidus. (To C. Cod.)
A. Smithii, nov.
A. Sebæ.
A. Ordwayi.
A. depressifrons.
Stenorhynchus sagittarius.
Podochela Riisei.
Mithrax forceps.
Macrocœloma trispinosum.
Calappa marmorata.
Petrolisthes armatus.

FIG. 5. *Parthenops crenulatus*; × about 3. Phot. A. H. Verrill.

Several of the species, mostly grapsoids, are found in most, or all, tropical seas, as well as in the West Indies. They are as follows:

Grapsus grapsus.
Geograpsus lividus.
Plagusia depressa.
Percnon planissimum.

Pachygrapsus transversus.
Planes minutus.
Domecia hispida.
Petrolisthes armatus.

Nearly all the widely distributed species, included in the last list, are found on the West Coast of Africa. But some additional species, common to Bermuda and the West Indies, are also found on the West African coast. Namely:

Goniopsis cruentatus.
Callinectes marginatus ? larvatus.
Stenorhynchus sagittarius.
Calappa marmorata.
C. gallus, galloides.
Hippa cubensis.

Aside from the widely distributed grapsoid crabs, found in all tropical seas, very few of the Bermuda species are found on the Pacific coasts of Central and North America. But some others are represented there by closely allied species or subspecies. The species that have been considered identical by recent good authorities are as follows:

Goniopsis cruentatus.
* *Grapsus grapsus.*
* *Geograpsus lividus.*
* *Pachygrapsus transversus.*
* *Planes minutus.*
* *Plagusia depressa.*
* *Percnon planissimum.*
* *Domecia hispida.*
Epialtus bituberculatus (varieties).
* *Calappa gallus* (varieties).
Cycloës Bairdii (varieties).
. *Petrolisthes armatus.*

Those preceded by an asterisk are circumtropical.

It is well known that a considerable number of species of Mollusca, Echinoderms, Anthozoa, etc., as well as Crustacea, are common to West Africa, Brazil and the West Indies. Such species may have originated on the African coast and thence migrated across the Atlantic to South America, and thence northward to the West Indies, Florida and Bermuda, during recent geological times. All the species of Decapod Crustacea having this wide range exist for a considerable length of time as free-swimming larval forms, in the zoëa and megalops stages. These larval forms may be carried long distances by the prevailing oceanic currents, especially in the regions of the trade winds.

It is scarcely admissible to suppose that they could have

traveled in the opposite directions, against the currents, unless by human agency, in recent times.

Many Crustacea, including the higher and more active forms, especially the grapsoid and cancroid crabs, are in

Fig. 6. *Cycloes Bairdii*, var. *atlantica*, nov., $\frac{9}{10}$ nat. size. Phot. A. H. Verrill.

the habit of hiding among the clusters of barnacles, etc., attached to the bottoms of vessels, and in this way they may be carried across the oceans in any direction, so long as the temperature of the water is suitable for their existence. In this way many tropical species reach the New England coast in summer, but die out during the winter.

Several species of crabs and shrimps habitually live among floating *sargassum*, or attached to floating drift-

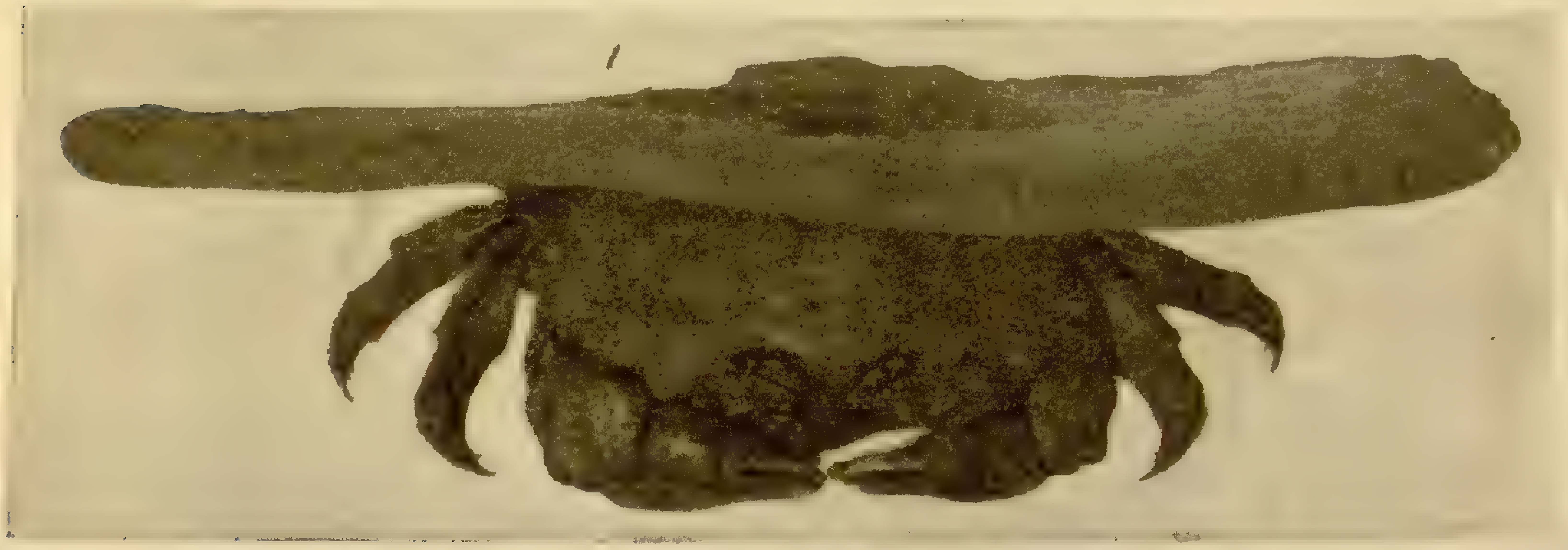

Fig. 7. *Dromia erythropus* from Dominica, with a flat Chalinid sponge held over its back, about ½ nat. size. Phot. A. H. Verrill.

wood. This is the case especially with *Planes minutus*, *Portunus Sayi*, and some others. That they have migrated to Bermuda in this way is very evident, for they do so constantly, day by day, at the present time.

But the majority of the species common to Bermuda and the West Indies do not have such habits, and must have migrated northward in the free-swimming larval stages. The directions of the Gulf Stream and prevailing wind currents are favorable for the transportation of free-swimming animals from the Bahamas, Cuba, etc., to the Bermudas.

On the other hand, very few, if any, strictly East American species have established themselves in the Bermudas, notwithstanding the constant passage of vessels in that direction for nearly three hundred years. Perhaps the temperature of the Gulf Stream is too high to allow such species to be carried across it, or they may not be able to endure the summer temperature of the Bermuda waters.

There are, likewise, no Decapod species of European or Mediterranean origin known in the Bermuda fauna, though such are known to occur in other orders, especially in those groups that habitually cling to the foul bottoms of vessels.

It would be of great scientific interest, as well as evident economical benefit, to experiment with the introduction of edible East American and West Indian crustacea that do not now exist at the Bermudas. Among those that might succeed are the large southern rock crab (*Menippe mercenaria*); the West Indian rock crab (*Carpilius corallinus*); the southern variety of the edible blue crab (*Callinectes sapidus*); and many others. Probably their fertilized eggs could be transported far more easily than the adults, and in vastly greater numbers. With suitable arrangements at the new Bermuda Biological Station, such eggs could easily be hatched and the young liberated in great numbers, in suitable places.

It would probably be useless to attempt to introduce those species that are restricted to our coast north of

Cape Hatteras, such as the common lobster, but there seems to be no reason why any species from the Carolina coasts or the Florida Keys should not flourish in Bermuda if once introduced there in considerable numbers and protected from their enemies at first.

Probably hundreds of species have been accidentally carried there, singly or in small numbers, in past times, which have failed to establish themselves, either because they became too far separated to find their mates at the breeding season, or because they were too soon eaten up by voracious fishes. Yet a single female crab, carrying fertilized eggs, might succeed in introducing the species, for their eggs often amount to 5,000, or even 10,000 at one time. Aside from edible species, the introduction of the smaller kinds would afford a large additional supply of food for useful fish, and thus benefit the fisheries.

ON THE INTERPRETATION OF CERTAIN TROPISMS OF INSECTS [1]

CHARLES THOMAS BRUES

MILWAUKEE PUBLIC MUSEUM

THE great interest which has developed among zoologists during recent years regarding the behavior of animals has resulted in such a large number of papers on tropisms and related topics, that a short discussion of the matter in regard to insects may seem rather uncalled for at present.

The field of entomological research affords, however, so many possibilities in this line that the activity which was formerly confined to studies of lower invertebrates is gradually showing a tendency to shift or to widen out toward the insects in its search for fresh subjects, and already the reactions of various species belonging to several groups have been investigated by the commonly accepted methods. The problem of studying the responses of insects to light, gravity, mechanical stimuli, etc., involves so many factors which do not enter into any consideration of simple organisms like protozoa or planarians that its complexity is rarely appreciated by those who give it their attention. The former animals can be brought into the laboratory and placed where the normal conditions of their natural environment are reproduced more or less faithfully. Under such circumstances their reactions and behavior can be analyzed by means of different mechanical contrivances which have been devised to test the influence of certain stimuli to the exclusion of others. To be brief, experience has shown that conclusions derived from such experiments are fairly trustworthy, and that a close approach can be thus made

[1] A paper read before the joint meeting of the Wisconsin Academy of Sciences, Arts and Letters and the Wisconsin Natural History Society at Milwaukee, February 13, 1908.

to an understanding of the animals' behavior in their natural environment. The extension of these methods into the study of such highly specialized and delicately organized invertebrates as insects is fraught by many dangers, and the failure to recognize certain inherent difficulties must inevitably invalidate some of the general conclusions which have been recently announced.

Without reference to the psychological aspect of insect behavior which I am in no way competent to consider, there are a number of factors entering into the study of reactions which I believe must be recognized if we are to appreciate the fundamental difference between a natural environment and an artificial reproduction of its single features in the laboratory.

Probably more experiments on insects have been recorded which bear upon the phenomena of phototropism than upon any other single tropism, and we may therefore reasonably suppose that the results in this field represent actual conditions as well as, if not better than, those on other tropisms.

Turning to a recent paper by Frederick W. Carpenter on the reactions of the pomace-fly, *Drosophila ampelophila*, to various stimuli,[2] we see the statement:

> "Light has both a kinetic and directive effect. The insect moves toward the source of light, being positively phototropic. The directive effect is apparent only when the kinetic stimulus is sufficient to induce locomotion."

This is merely a concise expression of the fact which we have all observed many times of the fly buzzing on the window. Under such conditions most Diptera are positively phototropic and will go through long series of alternating periods of activity and quiescence, the former usually induced by some external stimulus; attempting all the while to pass through the window toward the source of illumination. With many species this may often continue until the death of the insect from exhaustion and lack of food.

[2] AMERICAN NATURALIST, vol. 39, pp. 157–171, 1905.

Such are the results of experimentation where the transparent sheet of glass has been allowed to change the normal conditions of environment. Let us suppose, however, that the fly be allowed to pass out of the window into a more nearly natural environment. It immediately flies into the open, but does not endeavor for any length of time to continue its positively phototropic movements. Once unrestrained it is soon again following the normal pursuits of its particular species, which in the case of the aforementioned Drosophila is principally to locate decaying vegetable matter which will be suitable for food, breeding, and oviposition. It is evident in this case that the universal and quick response of the Drosophila to light when confined is due to some added factor in the experiment which I hope to point out on a later page.

Another paragraph in the same paper refers to results obtained under still more unnatural conditions.

> "The exposure of Drosophila to light of high intensity is accompanied by an increase in the kinetic effect. Under the influence of the highest intensity used, that of a 250 c.p. arc light at 40 cm., the muscle reflexes of an insect become very rapid and violent, and the directive influence of the light seems inhibited."

When we realize that these insects are as quick as ourselves to appreciate sudden changes in light and shade at short distances, it is not astonishing that they are unable to orient themselves under such startlingly unnatural conditions, placed only sixteen inches from an arc light, and their behavior here can not be compared with their reactions to normal daylight or sunlight. In fact the perversion of instinct induced by electric arc lights is a common experience with many nocturnal insects which are attracted in countless numbers, while their normally phototropic diurnal relatives are disturbed scarcely at all by the presence of the lights.

This too, is a matter of common experience, which has found expression in the adage of the moth and the flame. Most of the *Lepidoptera heterocera* are negatively phototropic, venturing out at dark and concealing themselves

from the light during the day, yet the proximity of an unnaturally brilliant light quickly upsets their normal instincts, and they are irresistibly attracted, although the appearance of the moon or the dawn affects them in no such manner.

Another tropism which is easily investigated by experimental observation is geotropism, and the agreement reached by a number of workers is that many insects when confined in an unnatural environment are negatively geotropic. To quote again from the same paper on Drosophila:

"Gravity has a directive effect upon the active insect which is negatively geotropic, that is, the insect moves away from the center of the earth."

Such is indeed the action of almost any insect, particularly an active species or a flying one when placed in any sort of a receptacle where it is deprived of food, or where it can not enjoy the freedom to which it is accustomed. It immediately flies or crawls upward, and usually will repeat the process almost indefinitely if for any reason it finds itself again at the bottom. Since it always goes to the top of the jar if not attracted in another direction by other stimuli, negative geotropism is taken to be one of its normal attributes.

This negative geotropism, however, becomes an absurdity as soon as we attempt to apply it in a general way to insects in their natural environment. Crawling insects do not congregate at the tops of objects in their environment, and neither do flying insects approach high altitudes, far from the surface of the earth. After their first escape from unnatural restraint, their negative geotropism vanishes as quickly as did their positive phototropism. The effect of any sudden and unnatural disturbance on the action of a flying insect is very easy of observation and is experimentally tested many hundreds of times during a season by any active collector of insects. Take, for example, a common bumblebee, which on account of its large size can be easily followed by the eye

as it passes from flower to flower, often traversing a considerable space in a nearly straight line toward a particular plant whose location may be known to it through past experience. Thus it continues along, sometimes rising slightly or flying lower, but exhibiting no movements whatever which could be attributed to geotropism or phototropism.

Let it be caught in the collector's net, however, and it immediately develops the negative geotropism, flying wildly about and seeking to ascend. If the net be kept inverted it will not escape until it accidentally drops out as a result of flying at the cloth of the net or of losing its foothold in crawling upward. Once out, it soars upward perhaps a short distance, and then resumes its former occupation.

Do these actions of the fly and the bee when confined, which are characteristic of other insects as well, represent their normal tropisms?

It has been usually assumed that they do, and several ingenious explanations have been suggested which endeavor to show why phototropism and negative geotropism become inactive in nature after certain periods, since the logical result of their continued action never presents itself to observation.

From the behavior of species in nature, these are most certainly not normal and are evidently caused by the conditions of the experiment. The most probable explanation of their appearance is that they are the expression of an instinct to seek the open whenever disturbed. In nature this freedom can always be obtained by flying upward and toward the light, that is to say, by phototropic and negatively geotropic movement which carries them away from all obstacles. Such a reflex in response to disturbances is a very valuable one and is no doubt maintained by natural selection, since it automatically offers an avenue of escape from disturbing conditions or danger.

In some species this reflex is in another direction, and these exceptions are most instructive in support of this

idea. Bees of the parasitic genus Cœlioxys when caught in the net almost invariably fly downward at the first impulse, being thus positively instead of negatively geotropic. A reason for this adaptation can be suggested from a knowledge of their habits. Graenicher[3] has recently shown that Cœlioxys enters the nests of other bees to lay its eggs. Thus in the event of its discovery by the rightful owner of the nest, it may drop to the ground with much better chances for escape than it would otherwise have.

Tiger beetles of the genus Cicindela are active fliers, but are more at home on the ground, consequently when covered by the net they never rise on the wing, but invariably attempt to escape on the surface of the ground, which they can readily do if the net does not fit very closely. Their actions can thus be traced directly to an adaptation.

From any unbiased review of such facts, I think it will appear that we can not hope to make wholly satisfactory progress along the line of interpreting insect behavior by means of studying their responses to stimuli in the laboratory, unless this be done with careful reference to their habits and behavior in nature, and in relation to the various external factors of their environment.

[3] *Bull. Wisconsin Nat. Hist. Soc.*, vol. 3, p. 162, 1905.

THE EVOLUTION OF TERTIARY MAMMALS, AND THE IMPORTANCE OF THEIR MIGRATIONS

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Third Paper.[1] Miocene Epoch.

After having investigated the migrations of the *Eocene* and *Oligocene* epochs (*Comptes rendus,* 6 novembre, 1905, et 12 mars, 1906), I will now consider those of the *Miocene.*

C. Miocene Fauna.—I. Lower Miocene (*Burdigalian*), fauna of the *sands of the Orléanais:* principal localities (Neuville-aux-Bois, Marigny, Rebréchien, Fay-aux-Loges, Beaugency, Tavers, Les Barres; Chevilly, Neuvilly, Artenay, Ruan, Chilleurs, Suèvres, Pontlevoy, Thenay, Blasois, Chitenay; Manthelan, etc.), and of the *limestone of Montabuzard,* underlying the sands.—The marine deposits of Eggenburg and Linz (Lower Austria), of the "*Muschelsandstein*" of Bruttelen, Macconens, La Molière, Bucheggberg (Switzerland), of Saint-Nazaire-en-Royans (Drôme), of the white Molasse of Angles (Gard), of Horta de Tripas near Lisbon.—Fauna of the fissures of the *Solenhofen* quarries.

1. *Local Evolution.*—Continuance of Tapiridæ (Paratapirus), of some genera of Rhinocerotidæ (Aceratherium, Diceratherium), of Chalicotheriidæ (Macrotherium), of Anthracotheriidæ (Brachyodus becoming extinct), of Suidæ (Palæochœrus, Hyotherium), of Tragulidæ (Hyæmoschus), of Cervulinæ (Palæomeryx, Dicrocerus), of Castoridæ (Steneofiber), of Cricetinæ (Cricetodon), of Lagomorph Rodentia (Prolagus), of Talpidæ (Talpa), of Tupaiidæ (Galerix), of Canidæ (last of

[1] Extract from the *Comptes rendus des séances de l'Académie des Sciences,* t. CXLIII, p. 1120 (séance du 24 décembre, 1906). Translated by Johanna Kroeber. First and second papers, Eocene and Oligocene, in the February and March numbers of the Naturalist.

Cephalogale), of Amphicyoninæ (Amphicyon), of Mustelidæ (Stenogale, Palæogale, Stenoplesictis), of Lutrinæ (Lutrictis, Lutra), of Felidæ (Pseudælurus, Machairodus).

2. *Very Important African or Afro-Asiatic Migrations* of Proboscidea (Mastodon, Dinotherium), of Antilopinæ (Protragocerus), of certain Cervulinæ (Micromeryx), of some Rhinocerotidæ (Teleoceras, Ceratorhinus), of some Suidæ (Chœrotherium, Listriodon), and of anthropoid apes (Pliopithecus).

3. *North American Migration* of Equidæ (Anchitherium).

II. Middle Miocene (*Vindobonian,* divisible into three substages: *Helvetian, Tortonian, Sarmatian*). Corresponding to these three substages are three mammalian faunæ, grading into one another by almost imperceptible transitions. These assemblages may be denoted as follows, the names being derived from those localities in the sub-Pyrenean basin where each is typically represented: (1) *horizon of Sansan,* (2) *horizon of Simorre,* (3) *horizon of Saint-Gaudens.*

1. *Horizon of Sansan.*—Principal localities: Sansan, Jegun (Gers), calcareous marls of the Loire (Pontlevoy, Sainte-Maure, Manthelan); marine Molasse of the environs of Romans (pont de l'Herbasse, Bren, Clérieux); marine Molasse of Suabia (Baltringen, Rammingen, Heggbach, Hausen; Niederstozingen, Süssen, Ursendorf, Hochgeland); of the lignites of Styria (Eibiswald, Göriach, Wies, Voitsberg, Gamlitz, Parschlug, Neufel) and of Lower Austria (Leoben, Leiding, Feisternitz, marine sands of Grund at Guntersdorf); Georgengsmund (Bavaria), Engelswies (Baden).

2. *Horizon of Simorre.*—Principal localities: Simorre, Bonnefond, St. Cristan, Tournon, Villefranche d'Astarac, l'Ile-en-Dodon (Gers); Saverdun (Ariège); marine deposits of Mirabeau (Basses-Alpes), of Sorgues (Vaucluse), of Romans (Drôme); Steinheim, Nordlingen, Ries, Althausen, Urlau (Suabia); Hohenhoven (Baden); intra-

Alpine basin of Vienna (Dornbach, Vordersdorf, Fünfkirchen, Loretto, Bruck-a.-Leitha, Breitenbrunn, Margarethen, Mannersdorf, Neudorf); Abstdorf, Franzensbad (Bohemia); Wosskressensk (Russia); Pesth, Ssoskut (Hungary); Trauenzinen (Silesia), Krivadia and Gyulu-Mendru (Transylvania).

The rich "terrain sidérolithique" ("Bohnerz") of La Grive-Saint-Alban (Isère), of Mont Ceindre (Rhône), of Pretty near Tournus (Saône-et-Loire), of Gray (Haute-Saône), of Mösskirch, Genkingen, Willmardingen, Heuberg, Melchingen, Jungnau (Suabia) belong in large part to this horizon.

3. *Horizon of Saint-Gaudens.* — Principal localities: Valentine, Saint-Gaudens, Montréjau (Haute-Garonne); Delsberg, le Locle, La Chaux-de-Fonds, Vermes, Oeningen, Ellg, Kapffnach, Weltheim (Switzerland); Hœder, Dinkelscherben, Günsburg, Diessen, Reichenau, Reisensburg, Dasing, Fraising, Tutzing, Stätsling, Reichertshofen, Frontenhausen, Flinz of Munich, Sankt Georgen (Bavaria); Hernals, Heiligenstadt (Vienna basin); Mt. Bamboli (Tuscany); San Isidro near Madrid; Aveiras de Baixo (Portugal); Kriwoi-Rog, Nicolaieff, Sébastopol, Tiraspol (Russia).

1. *Local Evolution.*—Continuance of Equidæ (Anchitherium), of Tapiridæ (Paratapirus), of Rhinocerotidæ (Aceratherium, Teleoceras, Ceratorhinus), of Chalicotheriidæ (Macrotherium), of Suidæ (last representatives of Hyotherium and Chœrotherium; Listriodon; finally Sus itself), of Tragulidæ (Hyæmoschus), of Cervulinæ (Dicrocerus, Micromeryx, last representatives of Palæomeryx), of Antilopinæ (Protragocerus), of Proboscidea (Mastodon, Dinotherium), of Theridomyidæ (last remnants of Theridomys), of Myoxidæ (Myoxus), of Sciuridæ (Sciurus), of Castoridæ (Steneofiber), of Cricetinæ (Cricetodon), of Lagomorph Rodentia (Prolagus, Lagomys), of Talpidæ (Talpa, Proscapanus, Scaptonyx), of Myogalidæ (Myogale), of Tupaiidæ (last of Galerix and Lantanotherium), of Soricidæ (Sorex, Crocidura).

last Dimylidæ (Plesiodimylus), of Erinaceidæ (Erinaceus, last of Palæoerinaceus), of Chiroptera (Rhinolophus, Cynonycteris, Vespertilio, Vesperugo), of Canidæ (Galecynus), of Amphicyoninæ (Pseudocyon, Hemicyon, Dinocyon, last Amphicyon), of Mustelidæ (Haplogale, Stenogale, Pseudictis, Mustela, Palæogale, Proputorius, Trochictis, Trochotherium), of Lutrinæ (Lutra, Enhydriodon), of Viverridæ (Viverra, Herpestes, Progenetta), of Felidæ (Machairodus, Hyænailurus, last Pseudælurus, first true Felis).

2. *Migration of South American origin* (by way of Africa) of the Hystricidæ (Hystrix).

3. *Migrations, Probably Asiatic-African,* of the Ursidæ (several branches, Pseudarctos, Hyænarctos, Ursavus), of the catarrhine monkeys (Oreopithecus), and anthropoids (Dryopithecus).

III. Upper Miocene (*Pontian*). *Fauna of Pikermi.*—Principal localities: Pikermi (Greece); Isle of Samos (Asia Minor); Maragha (Persia); Tchernigow, sands of Balta, limestone of Odessa and of Groussolowo (Russia); Manzati (Roumania); Baltavar, lignites of Baróth-Kôpecz (Hungary); Eppelsheim (Germany); Siebenhirten, Congeria gravels of the Vienna basin, vicinity of Eggenburg (Lower Austria); Mont Luberon, Visan (Vaucluse), Aubignas (Ardèche), Puy-Courny (Cantal), Saint-Jean-de-Bournay, La Tour-du-Pin, La Trappe de Chambaran (Isère), Montmirail, Tersanne (Drôme), La Croix-Rousse and Sainte-Foy à Lyon, Ambérieu, Soblay, Saint-Jean-le-Vieux (Ain), rocher du Dragon at Aix-en-Provence, Montredon (Hérault), Estavar (Cerdagne), Orignac (Hautes-Pyrénées); Concud (Spain); Archino (Portugal); Grasitelli (Sicily).

To the same horizon belongs the greater part of the "terrain sidérolithique" of Salmendingen, Melchingen, Trochtelfingen, Ebingen, Undingen, Heuberg (Suabia).

1. *Local Evolution.*—Continuance of Tapiridæ (Tapirus), of some groups of Rhinocerotidæ (Ceratorhinus,

last Aceratherium and Teleoceras), last Chalicotheriidæ (Chalicotherium), of Suidæ (Sus, last Listriodon), of Tragulidæ (last Hyæmoschus), last Cervulinæ (Dicrocerus, Micromeryx), of Castoridæ (last Chalicomys, earliest Castor), of Hystricidæ (Hystrix), of Canidæ (Simocyon), last Amphicyoninæ (Dinocyon), of Ursidæ (Hyænarctos, Ursavus), of Mustelidæ (Mustela, Promeles, Promephitis), of Viverridæ (Ictitherium), of Felidæ (Machairodus, Felis), of anthropoid apes (Dryopithecus, Anthropodus).

2. *North American Migrations* (perhaps by way of Asia) of one of the Equidæ (Hipparion) and of the Leporidæ (Lepus).

3. *Afro-Asiatic Migrations* of some Rhinocerotidæ (Atelodus), of Cervidæ (Capreolus), of Giraffidæ (Helladotherium, Palæotragus, Camelopardalis, Samotherium), of several groups of Antilopidæ (Palæoryx, Gazella, Palæoreas, Protragelaphus), of Ovidæ (Criotherium), of Hyænidæ (Lychyæna, Hyænictis, Hyæna), of Muridæ (Acomys), of catarrhine monkeys (Mesopithecus).

ON XEROPHYTIC ADAPTATIONS OF LEAF STRUCTURE IN YUCCAS, AGAVES AND NOLINAS[1]

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ZOOLOGY and botany are now so separated, and for a worker in one field to venture into the other is so unusual that it may not be out of place to state my reasons for presenting this paper, which are as follows:

1. Practically all of the material was worked up in 1903–4, and since I shall not have opportunity to complete the study I wish to make this part available.

2. I wish to emphasize the importance of the results of plant physiology to the zoologist. Many of those phenomena now brought into such prominence in zoology (*i. e.*, trophisms, heteromorphosis and the mutually antitoxic action of sodium and calcium) were discovered in plants and later studied in animals. Likewise the study of the water economy of desert plants may ultimately throw some light on similar processes in animals that are subjected to constant (*i. e.*, Dermestes) or periodic lack of water (*i. e.*, rotifers). The cutin of plants and the chitin of animals play similar rôles, and it may be that the carbohydrate and mucoid (?) water-storing substances in plants have analogues in animals.

I am indebted to Dr. W. L. Bray for suggesting and directing this study, and for procuring the material, most of which he obtained from Langtry, Texas and from the Missouri Botanical Garden.

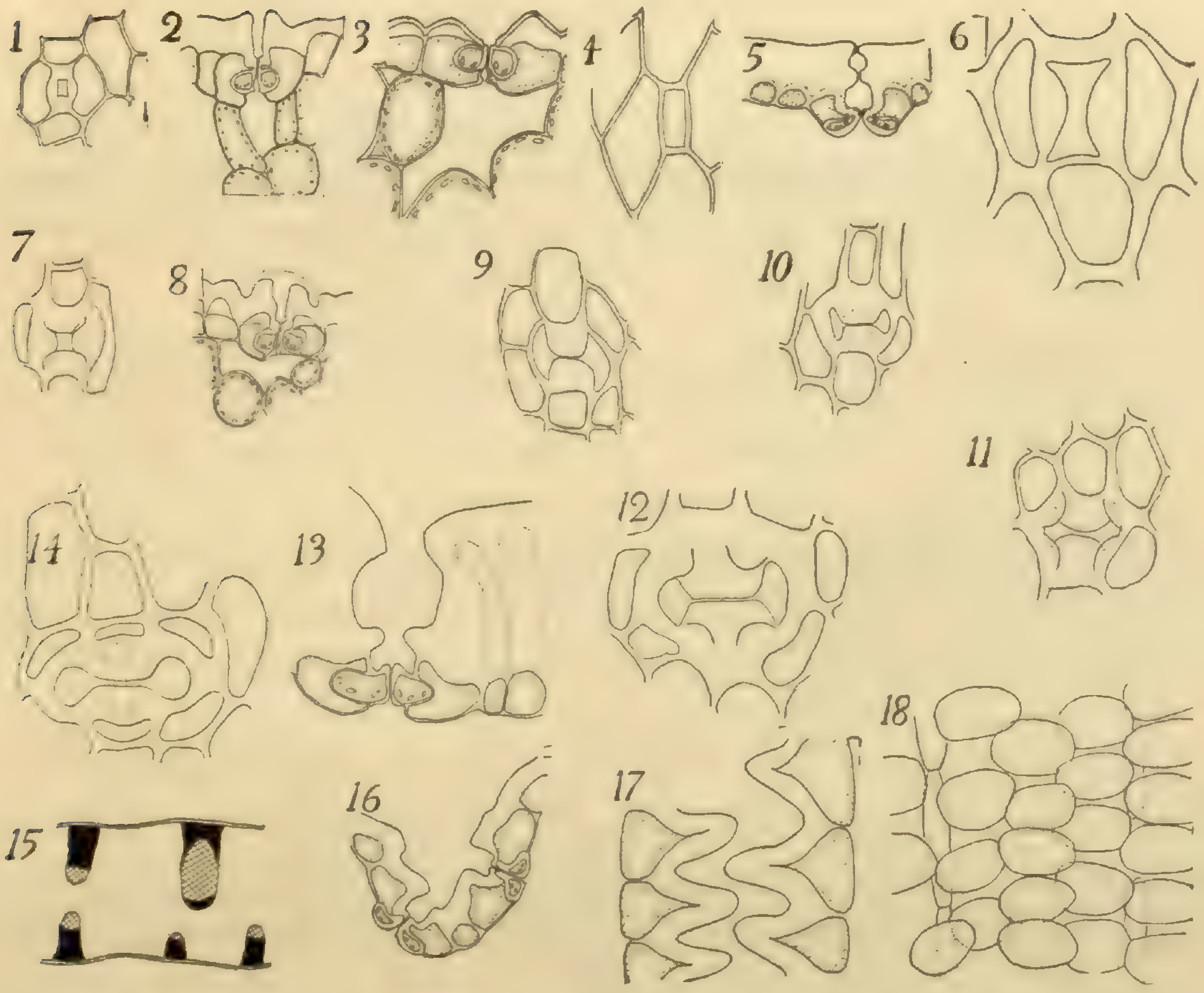
Methods.—The most serviceable method for investigating cell walls was free-hand sections stained in chlorio-

[1] Contribution from the Botanical Laboratory of the University of Texas under the direction of Dr. W. L. Bray.

dide of zinc. A freezing microtome might have been of service. Celloidin did not penetrate thoroughly in six weeks and was abandoned. Thin paraffine sections were cut, but where bundles were isolated in succulent tissue they usually tore through part of the latter. The experimental side of the subject was not touched.

Yucca and its allies are mostly xerophytic plants that have been modified along various lines to adapt them to their xerophytic habitat. Root, stem and leaf are succulent, thus serving for water-storage tissue. The leaves are closely set in a rosette, thus protecting one another against too great insolation and transpiration. In Agave, Hesperaloe, Dasylerion, Nolina and some species of Yucca the stalk is very short, thus enabling the leaves to shade the ground over the larger roots and protect them from drying. The leaves are especially modified: the epidermis is greatly thickened and heavily cutinized, the skeleton more or less rigid, the stomata sunken beneath the surface, either singly or in grooves, and the assimilation tissue many layers thick.

The Respiration System.—The simplest type of stoma in this group is probably found in *Yucca aloifolia tenuifolia* (Figs. 1 and 2). In this species the guard cells are not sunken much beneath the general epidermal surface, but the very thick epidermis is pierced by an air passage nearly square in cross section (Fig. 1), leading to the slit between the guard cells. Beneath the guard cells is an intercellular air space of considerable size leading into small intercellular air spaces. The epidermis is heavily cutinized and the cutin extends inward through the stoma and lines the upper part of the air space beneath. The assimilation tissue is palisade near the epidermis; but the cells show a tendency to arrange themselves radially around the vascular bundles. There are large intercellular air spaces in the interior of the leaf. Stomata of like character were found in *Yucca aloifolia, Y. aloifolia marginata, Y. aloifolia conspicua, Y. gloriosa* and *Y. gloriosa flexilis.*



(In diagrammatic cross sections mechanical tissue is black and vascular tissue cross striated.)

FIG. 1. Stoma of *Yucca aloifolia tenuifolia*—surface view.
" 2. The same in cross section of leaf.
" 3. Stoma of *Agave yuccæfolia* in cross section of leaf.
" 4. Same—surface view.
" 5. Stoma of *Dasylerion texanum* in cross section of leaf.
" 6. Stoma of *Agave americana*—surface view.
" 7. Stoma of lower side of leaf of *Yucca recurvifolia*—dotted lines represent portions of two teeth that are covered by the other two.
" 8. Same in cross section of leaf.
" 9. Stoma of *Yucca radiosa*—surface view.
" 10. Stoma of *Y. rostrata*—surface view—passage beneath teeth shown by dotted line.
" 11. Stoma of *Y. glauca*—surface view.
" 12. Stoma of *Agave victoria reginæ*—surface view.
" 13. Stoma of same in cross section of leaf.
" 14. Stoma of *A. schotti*—passage beneath teeth shown by dotted line.
" 15. Diagram of part of cross section of leaf of Nolina sp.? from Mexico.
" 16. Groove in cross section of leaf of *Dasylerion glaucophyllum*.
" 17. Groove in tangental section of leaf of *Nolina texana*.
" 18. Assimilation tissue in longitudinal section of same.

In *Agave yuccæfolia* the cutinized layer of the epidermis is thinner and the air passage leading to the stoma proper is much shorter than the preceding and is elongated parallel to the long axis of the leaf (Figs. 3

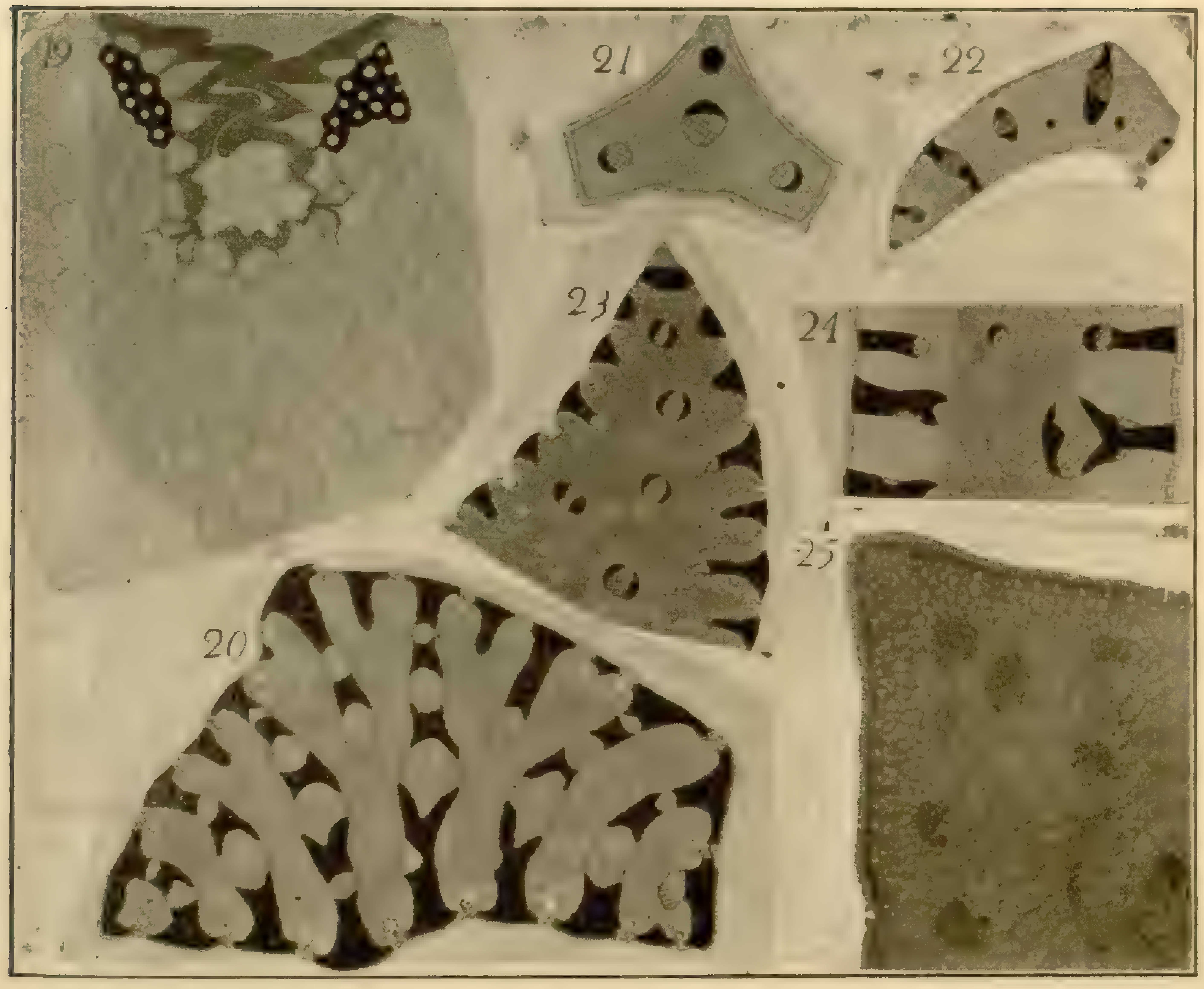


FIG. 19. Groove in cross section of same—the cutinized portion of epidermal cell walls shown darker than other cell walls; mechanical tissue black.
" 20. Cross section of leaf of same.
" 21. Cross section of leaf of young seedling of same.
" 22. Same after two years growth in damp greenhouse.
" 23. Part of cross section of leaf of *Hesperaloe parviflora*.
" 24. Part of cross section of leaf of *Dasylerion wheeleri*; the middle of the leaf is filled with large celled storage tissue.
" 25. Part of cross section of leaf of *Agave strida*—photograph.

and 4). Beneath the cuticle is a thick layer of water-storing cellulose. A series of forms with this type of stoma arranged in order of progressive sinking of the stoma would include: *Hesperaloe præciosa, Yucca de smetiana, Y. rupicola, Agave strida* and *Dasylerion texanum*. In the last named (Fig. 5) the supra-stomal passage is divided into two dead air spaces, and the stomata occur in slight longitudinal furrows. The ridges between are braced heavily with mechanical tissue.

In *Agave americana*, the century plant (Fig. 6), the sides of the elongated supra-stomal passage are produced into lips, constricting it in the middle.

In *Dasylerion wheeleri* a second similar constriction occurs half way down this passage, so that in cross section it appears like *Dasylerion texanum.* In this species the epidermal cells are produced into papillæ.

Going back to the simple type of stoma found in *Yucca aloifolia* we can trace variation in another direction. In the stomata of the lower side of the leaf of *Yucca recurvifolia* the four sides of the supra-stomal passage are produced into lips; those parallel to the long axis of the leaf being beneath the others (Figs. 7 and 8). On the upper side of the leaf the lips are not as well developed, and are all in the same plane, as are also those of *Yucca australis* and *Y. treculiana.*

In *Yucca radiosa* (Fig. 9) and *Y. constricta* only two of the lips are developed, so that we have an opening somewhat like the ones in *Agave americana* rotated through a right angle. In *Yucca rostrata* the lips have developed so as to close the opening in the middle, leaving only an opening at each end (Fig. 10).

In *Y. glauca* (Fig. 11) four additional lips have developed above the two as in *Y. radiosa,* and the accessory cells have sunken considerably beneath the level of the other epidermal cells.

In *Agave victoria regina* (Fig. 12) the presence of six lips is accompanied by the meeting of one pair and by the division of the supra-stomal passage into two dead air spaces (Fig. 13). Here the epidermal cells secrete an immensely thick layer of reserve or water-storing (?) cellulose under the cuticle (Fig. 13). The leaf is very succulent and the vascular bundles are confined to the middle layer.

In *Agave schotti* the shape of the supra-stomal passage changes greatly as we go inward. On the surface it is elongated at right angles to the long axis of the leaf, while farther down it is elongated parallel to the long axis (Fig. 14).

Besides being sunken singly between the level of the

epidermis the stomata are often placed in rows at the bottom of a groove. These grooves are very slight in Nolina sp.? from Mexico (Fig. 15), *Dasylerion wheeleri* and *D. texanum*. They are deeper in *D. glaucophyllum* (Fig. 16) and *Hesperaloe parviflora*.[2] They are very deep and guarded with teeth in *Nolina texana*[3] (Figs. 17 and 18) and Nolina sp.? from West Texas. The formation of grooves is directly associated with the bracing of the epidermis with beams of mechanical tissue (Fig. 20) along the ridges between the grooves. In Nolina sp.? from Mexico (Fig. 15), *Dasylerion wheeleri* (Fig. 24), *D. texanum* and *Hesperaloe parviflora* (Fig. 23) these beams are free in the interior of the leaf, but in *D. glaucophyllum* and *Nolina texana* (Fig. 20) the beams of one side usually meet and fuse with those of the other, forming a rigid support for the epidermis that prevents any dorso-ventral shrinkage of the leaf on drying. The only shrinkage that does occur closes the grooves and thus is a further check to transpiration. Another characteristic associated with the presence of these longitudinal transpiration grooves is a peculiar modification of the air passages in the assimilation tissue, which reaches its greatest development in the Nolinas. In the forms without grooves there is an irregular air space below the stoma, from which lead minute air spaces in all directions. With the development of grooves is associated a more effective arrangement of these air spaces, so that rapid respiration of the deeper tissue is effected without the devotion of much of the volume of the leaf to air space. If we imagine the groove represented in Fig. 17 in tangential section, as being placed horizontally with the opening upward, the assimilation tissue in the form of lamellæ one cell thick is suspended from the inner surface of the groove. Air diffusing in through the stomata enters the narrow spaces between the lamellæ and almost immediately penetrates to the center of the leaf. If we

[2] Bray, '03.

[3] Bray, '03.

imagine a lamella removed from the leaf when turgid, the cells composing it would be rounded on their free surfaces. If such a lamella were placed on another so that some of its cells rested on the apices of the cells of the one underneath, we should get a condition similar to that in *Nolina texana* (Figs. 18 and 19) and allied forms. Fig. 18 is drawn from a thick longitudinal section of the leaf, and the irregularities in the lamellæ obscure their distinctness. The lamellæ are additionally supported by columns of elongated cystoliths running parallel to the long axis of the leaf and connecting one lamella with another.

Mechanical and Vascular Tissue.—The leaves of Yucca and its allies are covered by a very thick cutinized epidermis which is quite stiff and supports the soft tissue beneath, thus forming an exoskeleton. In smooth leaves the bundles are distributed through the interior of the leaf, in thick leaves being arranged in several rows (Fig. 25). Each bundle is composed of vascular tissue supported by a large amount of mechanical tissue, and thus the bundles form an internal skeleton. In those leaves in which grooves occur the ridge between two grooves is heavily braced within with mechanical tissue (Fig. 23). These braces often extend inward until each fuses with a bundle (Fig. 23) and in some species all the bundles are attached to the inner edges of these braces (Fig. 15). In *Dasylerion glaucophyllum* and some species of Nolina (Fig. 20) the braces of one side of the leaf usually fuse in the middle with those of the other side, making a very rigid structure.

Relation of Habitat to Structure of Stoma.—The complexity in structure of stoma in these forms lead Dr. Bray to suggest that I see whether there was any correlation between the structure of the stomata and the aridity of habitat. I found that there was in all except those that had the supra-stomal passage much elongated in the long axis of the leaf. *Yucca aloifolia*, *Y. gloriosa* and their

varieties have a supra-stomal passage nearly square in cross section (Fig. 1) that goes straight down to the stoma, and these species inhabit coast lands which, although hot, are humid. In *Y. australis*, *Y. treculiana* and *Y. recurvifolia* the supra-stomal passage is guarded by four lips (Fig. 7) and these species inhabit a region from the Gulf coast to the dry interior of the United States and Mexico. In *Y. radiosa* and *Y. constricta* the supra-stomal passage is closed in the middle (Fig. 9) and these species inhabit southern Arizona, western Texas and adjacent country. In *Y. rostrata* two widely separated openings lead into the supra-stomal passage (Fig. 10), and we find this plant in the deserts of northern Mexico. In *Agave victoria regina* we find a similar structure with the addition of four small lips (Fig. 12) and we find this plant also in the deserts of northern Mexico (Coahuila). In *Yucca glauca* we find a structure similar to the preceding save that the two lower lips are slightly separated (Fig. 11), and this plant inhabits the slightly less arid lands from South Dakota to New Mexico and North Texas. In *Agave schotti* the supra-stomal passage is compressed in one axis (Fig. 14) and a little lower down is compressed at right angles to the first (Fig. 14, dotted line) and we find this plant in the deserts of southern Arizona. Finally, the Nolinas, whose stomata are placed in deep grooves guarded by interlocking teeth, cling to crevices in the rocks in western Texas and northern Mexico, where not only is the air dry and the sun hot, but there is extremely little soil to hold a store of moisture.

Development of Leaf in Nolina Texana.—The very young leaf in the adult plant is not deeply grooved as in Fig. 19 or 20 and the mechanical tissue is not well developed. The formation of grooves is associated with the formation of ribs of mechanical tissue supporting the epidermis between the bands of stomata, and by growth inward uniting with the vascular bundles, thus forming

girders extending through the leaf in a dorso-ventral direction. The epidermis bulges out along the lines of attachment of the girders and sinks in between them. The epidermal cells bordering the grooves thus formed grow out into long interlocking teeth. The teeth get longer and the groove narrower as the leaf develops, thus protecting the stomata from the dry air.

In the very young seedling the leaf is somewhat triangular in cross section (Fig. 21) with a vascular bundle in the center and one in each lateral angle and a bundle of mechanical tissue in the midrib. The epidermis is cutinized at this early stage.

I kept a seedling in a greenhouse of the University of Pennsylvania about two years. The leaves did not grow stout as in plants from the natural habitat and I think the increased moisture and diminished insolation affected the thickness of the leaves (Fig. 22). The leaves were very thin; the mechanical tissue uniting with the vascular bundles formed beams connecting the dorsal with the ventral epidermis between the bands of stomata, but the grooves only began to develop. It seems remarkable that a plant so adapted to xerophytic conditions should be able so quickly to adjust itself to a moist atmosphere, and I think the subject merits further investigation.

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THE BIOLOGICAL LABORATORY OF THE BUREAU OF FISHERIES AT WOODS HOLE, MASS.: REPORT OF WORK FOR THE SEASON OF 1907

DR. FRANCIS B. SUMNER

DIRECTOR OF THE LABORATORY.

I. RECENT IMPROVEMENTS IN EQUIPMENT, ETC.

1. Two rooms upon the third floor of the laboratory building have been reconstructed so as to serve for the reception of the specimens comprising the local reference museum. These last were moved from their former inadequate quarters at the commencement of the summer, and have been subjected to a thorough overhauling.

2. A considerable number of standard scientific works were purchased by the bureau as the nucleus of a permanent reference library; though it is true that only a beginning has thus far been made. The already great collection of reprints and other miscellaneous donations, together with the reports of the scientific departments of this and other governments, has steadily increased. It was found, however, that the publications of many of our foremost American biologists were scarcely represented on the shelves of the library. With a view to remedying this serious lack, a circular was sent by the director to about three hundred American men of science, chiefly biologists, asking for contributions. A considerable number of these men responded liberally, and many hundreds of pamphlets and bound volumes have been received. It must be added with regret, however, that many others among those addressed have not yet thought it worth their while to place their writings in an institu-

tion conducted solely for the public welfare, and offering free facilities each year to a large number of biologists.

3. A steam drying apparatus was purchased, at a total cost of over three hundred dollars, for use in experiments upon the methods of preparing various marine foods. Owing to serious delay on the part of the manufacturers, this apparatus was unfortunately not installed until late in the season.

4. Running fresh water was introduced into each of the large investigation rooms upon the second and third floors of the building, and enameled iron sinks were likewise installed in these rooms.

5. A contrivance was designed and constructed for the purpose of de-aerating the salt-water supply of the laboratory and aquarium.

6. The entire floor of the main laboratory room (162 square yards) was covered with a layer of heavy linoleum.

7. Electric table lamps, with parabolic reflectors, were substituted for the hanging lamps formerly used in the investigation rooms.

8. The supply rooms for apparatus and chemicals were greatly extended, and many improvements were effected by carpentry throughout the building.

II. Broader Lines of Investigation

1. *Biological Survey.*—Much progress was effected during the summer, as well as during the preceding winter, in the preparation of the report upon the biological survey of local waters. It has furthermore been necessary to extend this work through the present winter; and the director is again in residence at Woods Hole, engaged in the completion of this project. At the present time it may be stated that the plotting of the distribution charts, several hundred in number, has been nearly completed by Mr. J. W. Underwood; the compilation of an annotated list of the local fauna and flora (based both upon original observations and published records) is not

far from finished; the physical data (temperature, etc.) are being tabulated; and preparatory steps are being taken toward the statement of generalized results and conclusions. During the summer it was found necessary to repeat the temperature and salinity determinations of preceding years. The steamer *Fish Hawk* was employed for this purpose and recently standardized instruments only were used. In this work the director was ably assisted by Mr. D. W. Davis. Careful thermometry revealed temperature conditions which do much toward explaining the distribution of certain forms of life, especially of those well-known boreal types which just enter the region. This problem seemed of sufficient importance to justify another extensive series of temperature and density determinations at the commencement of the present winter, and these have therefore been made by the director, with the assistance of the crew of the *Phalarope*. A third series of observations is contemplated early in March; and possibly another at the commencement of the summer.

The *Fish Hawk* was also employed in doing considerable supplementary dredging; and the in-shore stations of Buzzards Bay, which, owing to an accident to the *Phalarope,* had been left unfinished in 1905, were now completed with the aid of the latter vessel. It is perhaps worthy of mention that the parasitic gastropod mollusk, *Stilifer stimpsoni* Verrill was taken for the first time (so far as recorded) in this region; and that the rare brittle star *Amphioplus abdita* (Verrill), which was recently made the subject of a special note in *Science*[1] by Dr. H. L. Clark, was dredged at no less than three stations.

With one or two exceptions, all past collections derived from the dredging operations have been reported on by the specialists to whom they were referred. More than half of the catalogue of fauna and flora has been submitted in manuscript form to these same taxonomic

[1] January 24, 1908.

experts for revision of nomenclature and other points. It is hoped that the entire report may be completed in the rough before the expiration of the coming summer.

As usual, a fish trap was maintained in Buzzards Bay, at a point not far distant; and the customary seining trips were made for the supply of laboratory needs, as well as to furnish data regarding the occurrence of species. As a fact of especial interest in relation to the local fauna may be mentioned the entire lack, during the past season, of the gulf-weed, and the accompanying stragglers from tropical waters, which frequently form such a striking feature of the marine life during the latter part of the summer.

2. *Studies of Marine Foods.*—Investigations have for several years been in progress, directed toward the utilization of certain marine organisms of apparently high food value, which have, notwithstanding, been hitherto neglected by our population. The "smooth" dogfish, the squid,[2] and the salt-water mussel have thus far received most attention at this laboratory. An arrangement was entered into with the "mess" of the Marine Biological Laboratory, whereby certain foods were prepared according to definite directions and served at certain of the dining tables. It was thus possible to obtain the opinions of a considerable number of persons as to the palatability of the articles in question. As already stated, a steam drying apparatus has been installed at this station as an important auxiliary to these experiments. Messrs. I. A. Field and C. L. Alsberg are engaged upon both the economic and the scientific aspects of this problem. Professor Field has already reported[3] upon certain features in the bionomics of the dogfish and some other unutilized fishes, but much work remains to be done, on both the industrial and the chemical phases of the subject.

[2] It is here worth mentioning that two representatives of a Japanese produce establishment spent the summer on Cape Cod, taking steps toward the establishment of a plant for the drying of squid for exportation to their own country.

[3] Bureau of Fisheries Document No. 622, issued 1907.

3. *Deaeration of the Laboratory Water Supply.*—The "gas disease" of fishes, especially as manifested in the aquaria at the Woods Hole station, has, in past years, been the subject of extensive investigations by Gorham and Marsh.[4] These two writers presented convincing evidence that the cause of this malady lay in the super-saturation of the salt-water supply with air. The latter was shown to be forced into solution under pressure, during the process of pumping, so that the water which passes into the distributing tanks is "charged" with air, in much the same manner as soda-water and other carbonated beverages are charged with carbon dioxid. It is a familiar fact that such beverages quickly become "flat" if left to stand in an open vessel; and that the discharge of the gas is facilitated by agitating the liquid. Marsh found that in this principle lay a ready means of preventing the troubles arising from the super-saturation of the Woods Hole water supply. If the water, before its entrance into an aquarium or fish tank, were allowed to splash through a perforated pan, or merely to fall from a height as a fine jet, the evils of the gas disease would be diminished or altogether prevented. This method has since been generally adopted at the laboratory in connection with the large aquaria employed for display purposes, as well as with the smaller ones used for scientific experiments. It has commonly been necessary to employ the smallest stream of water practicable, allowing it to fall from a height, and commonly causing it to pass through a perforated pan, or to trickle over a board or other flat surface. Indeed, there have frequently been occasions when a strong stream, introduced beneath the surface of the water in a small aquarium, would prove fatal within a day or less, even to hardy fishes.

Such a state of affairs has obviously been a serious drawback to the work of the laboratory, which often

[4] Bulletin U. S. Fish Commission, Vol. XIX (1899), pp. 33–37; Report U. S. Fish Commission for 1903 (1905), pp. 93–98; Report of the Bureau of Fisheries for 1904 (1905), pp. 343–376, pl. I–III.

demands that fishes shall be kept under observation, in a healthy condition, for days or weeks. Some method of treatment was deemed advisable which should be applicable to the water supply as a whole. Thus far, no attempts to prevent the entrance of air into the pump, along with the water, have been permanently successful. The wooden suction-pipe, through which the pump formerly received its supply of sea-water, was replaced, early in 1903, by a metal one, the assumption being made that the porous condition of the former was responsible for the trouble. Indeed, Marsh and Gorham, writing during the following year, declare that "the replacement of the old suction pipe with a new impervious one abolished all signs of the gas disease at Woods Hole." But the malady was again rife during the summer of 1905, and has given much trouble during the seasons of 1906 and 1907. In the absence of definite information as to the present source of the air in the water, the most promising mode of attacking the difficulty seemed to be the construction, on a large scale, of a *deaerator,* which should operate on the same principle as the pans and boards before employed for individual aquaria. Accordingly a series of five wooden trays was built, these lying in a zig-zag series, one above the other, and having a total bottom area of about 10,000 square inches, thus bringing a large surface of water into contact with the air. Perhaps the most effective factor in the case, however, is the splashing of the water in its descent from one trough to the other and from the lowermost of these into the supply tank below. From the latter the water is distributed to the laboratory.

This deaeration apparatus was not constructed until late in the past laboratory season, but the results of the tests already made seem well worth recording. The fatal effects of the water from the local supply had been conspicuous throughout the summer. It may be mentioned, by way of example, that in one wooden tank in the hatching room twenty tautog died in a single day, apparently

from this cause alone. In the display aquaria the fishes had fared pretty well, thanks to the use of perforated pans, which were suspended several feet above each tank. The water was in no case allowed to enter below the surface, as experience had shown that the result would have been disastrous. The deaeration apparatus was first put into use on August 31, and two days later the pans over these aquaria were removed, a full head of water being allowed to enter below the surface in each. This condition was maintained until September 23. During this period of twenty-one days no deaths occurred beyond those occasional ones to be expected in a large miscellaneous collection of living fish. No symptoms of the gas disease were noted, either in the presence of surface "blebs," or in the occurrence of "pop-eyed" fishes. The collection seemed in particularly good condition, and the absence of the splashing water overhead made it possible to keep the premises much more dry and neat.

The natural inference from these facts was that the deaerator had fulfilled its requirements perfectly. But before forming definite conclusions on this point, it was necessary to perform the control experiment of throwing the apparatus out of the circuit, and using the salt water just as delivered by the pump. This was done on the afternoon of September 23. The water supplying the aquaria was allowed to enter below the surface as before. On the following day (September 24) bubbles were noted upon the surface of some of the fishes, either in the mucus or beneath the epidermis. From records made throughout the ensuing twelve days, it appeared that out of 85 fishes, belonging to 18 species, which were present at the time the process of deaeration was discontinued, 13, or more than 15 per cent., died within the ensuing six days; while within the first twelve days 15 others, or nearly 18 per cent., manifested more or less marked symptoms of the gas disease. Almost exactly one third of the stock had accordingly been killed or obviously injured.

III. Seventh International Zoological Congress

One of the prominent features of the program for the entertainment of the congress was a visit to Woods Hole on Sunday, August 25, when the members were welcomed jointly by the Marine Biological Laboratory and the Fisheries Laboratory. After a lunch served in the "mess" hall of the former institution, the party was carried to New Bedford on the U. S. Fisheries steamer *Fish Hawk*. One drag with the dredge was made *en route* by way of demonstration. On the preceding evening an informal smoker was tendered by the research staff of the Fisheries Laboratory to the local scientific colony and to such of the foreign delegates as had already come to Woods Hole in response to a special invitation. Thirteen of these visitors[5] were housed for the night in the residence building of the station. A few of the most eminent of the foreign delegates, including Hubrecht, Bateson, von Graff and some others, had spent a week or more at Woods Hole prior to the visit of the congress; not, however, as the guests of this laboratory.

IV. Individual Researches

Of the twenty-five or more persons employed in various capacities on behalf of the laboratory, thirteen may, from the nature of their work, be ranked as investigators, the others serving as assistants, janitors, etc. Fourteen volunteer (unpaid) investigators likewise held tables and carried on independent lines of research. These twenty-seven investigators represented 11 states and 21 educational institutions,[6] ranging from New Hampshire to Michigan and Virginia. A detailed statement of individual researches is given below.

The hospitality of the station was likewise extended to a number of gentlemen who are not strictly to be enrolled

[5] Messrs. Derjugin, Golovine, Heymons, Koshewnikov, Kusnezov, Le Souëf, Maximow, Metalnikoff, Nedrigoiloff, Samssonow, Wladimiroff and two others (record lost).

[6] Each being accredited to the institution in which he had taught or studied during the preceding academic year.

among those conducting investigations in the laboratory during the past season. Among these are to be named the Hon. K. Gupta, of Bengal, who was making a study of American fisheries methods on behalf of his government; Messrs. G. Asaya and T. Miyake, who were seeking information in regard to the local occurrence of the squid; and Professors W. A. Locy, Henry F. Nachtrieb and S. P. Sigerfoos, who visited Woods Hole briefly at about the time of the zoological congress.

Carl L. Alsberg, M.D., instructor in biological chemistry, Harvard Medical School.—The greater part of Dr. Alsberg's work consisted in the collection and preparation for analysis of various marine animals which are either not used, or little used, as foods in this country. The complete analysis of such material was deferred until the winter months, when better facilities for analytical work would be available than it is possible to provide at Woods Hole. The work actually done at Woods Hole was to determine the water content of the different materials, as well as the proportion of soluble proteid, etc. The other analyses are now being carried out in Boston. As a result of this work, it has become evident that in order to obtain reliable information concerning the food value of many of these forms it is necessary to study the extractives. As is well known, the extractives of ordinary meats have but little food value. For some of the lower forms, notably the dog fish, this is true to an even greater degree, because this fish contains large quantities of urea dissolved in the blood plasma and in the body fluids. In order to arrive at a correct estimate of the food value of such an animal, it is necessary to determine by accurate methods the urea content, and perhaps also that of the other extractives. Concerning the extractives of other forms at present under investigation, for instance the squid, nothing at all is known, and it will be necessary to make a study of them before we can estimate the food value of this mollusk. In addition to this line of work,

which has immediate practical value, various other investigations were undertaken, or at least the material for such investigations was collected. The study of the blood of the horse-shoe crab was begun, and two researches have been subsequently completed in Boston, both of which were presented at Chicago during the present winter, one before the American Society of Biological Chemists, and the other before the American Physiological Society. The first deals with the study of the blood-clot of this animal; the second started with a study of the enzymes of the serum and has led indirectly to interesting results concerning the guajac reaction of peroxydases. Another investigation, the material for which was collected at Woods Hole, has also been finished subsequently. This is a study of the vitelline contained in the eggs of the spiny dog-fish. This vitelline has proved to be very similar to that which may be obtained from hens' eggs. Finally, an examination was undertaken, but not yet completed, into the nature of the red pigment contained in the chromatophores of the skin of the squid.

Charles B. Bennett, graduate student, Brown University, (1) took part in the work of the biological survey, being engaged in a search for certain marine organisms concerning which additional data were required, (2) assisted Dr. Alsberg and Professor Field in some of the work above described.

Walter B. Cannon, A.M., M.D., professor of physiology, Harvard Medical School.—*The Movements of the Alimentary Canal in the Dog-fish.* Peristaltic waves were seen to pass over the lower third of the cardiac end of the stomach, but they did not pass on to the pyloric end. Along the narrow pyloric portion the waves were more frequent than on the cardiac portion. Three movements were seen in the spiral valve: (1) A segmenting movement, starting anteriorly as a constriction, which was replaced by a constriction one centimeter below, and this

by another one centimeter below that, etc., until the whole intestine was traversed. When the series had passed three or four centimeters from the starting point, a new series began. (2) A movement starting posteriorly and passing forward, which consisted in a local shifting of the wall towards the left, *i. e.*, clock-wise with reference to the axis of the valve viewed from behind. As shown by small holes cut in the wall, the shifting of the wall towards the left was accompanied by a shifting of the inner folds towards the right. The effect must be a thorough mixing of the food between the two surfaces. (3) A large general shifting of the valve forwards, and with a right rotation through about 180°. This was caused by a great sheet of smooth muscle lying in the mesentery between the genital gland and the spiral valve.

Joseph F. Clevenger, M.A., acting professor of chemistry and biology, Wheaton College, Wheaton, Ill.—*The Life History of Zostera marina and Ruppia maratima.*

Harold S. Colton, M.A., graduate student, University of Pennsylvania.—*How "Fulgur" and "Sycotypus" eat Oysters, Mussels and Clams.* The work, so far as performed at Woods Hole, consisted of a series of experiments and observations on the food of Fulgur and Sycotypus (*Busycon carica* and *B. canaliculata*), supplementing some which were begun at the University of Pennsylvania during the preceding winter. There had previously been no complete account of the taking of food by those gastropods. Stimpson (1860) and Ingersoll (1884) have mentioned their food; the former not completely and the latter not correctly. The present studies dealt with the kind and amount of the food and their manner of taking it. (1) Although pieces of chopped oyster were found to stimulate these mollusks, the latter were never observed to eat them. *B. canaliculata* ate living Mya, Ostrea and Mytilus, but refused Venus. *B. carica* accepted Mya, Ostrea, Mytilus, Modiolus, Ensis and Venus,

and devoured one of each. (2) It was frequently found that one individual ate two oysters or clams in a day; there usually being a long period of rest between meals, the animal remaining buried nearly all the time, sometimes for as much as six weeks. (3) The character of the erosion, noticed on the odontophore, indicates that these mollusks are not shell borers. (4) When clams (Mya) are the objects of assault, no difficulty is encountered in gnawing out the soft parts, since the shells of the latter gape slightly. The mussel and oyster, on the other hand, are taken by surprise. The attacking gastropod thrusts the margin of its own shell between the valves of that of the prey, devouring the soft parts at leisure. In the case of the "round clam" (Venus), *B. carica* uses yet another method of attack. Holding the bivalve in the hollow of its foot it brings the margin of its own shell against the margins of that of its prey. By the contraction of the columellar muscle, the two are brought into such forcible contact that a small piece is chipped from the Venus shell. This is repeated many times, the process lasting from seven hours to three days, with the result that the crevice between the two valves is enlarged to such an extent that the gastropod can devour its victim. (5) It is possible that the two species of Busycon do not inflict so great damage upon oyster or clam beds as has previously been reported. Field observations alone can settle this point, however.

Edgar D. Congdon, M.A., Austin teaching fellow, department of zoology, Harvard University, conducted investigations upon the fauna of the brackish waters in the neighborhood of Woods Hole. A number of these ponds were studied intensively, collections being made of their fauna and flora, and determinations of density and temperature being taken. A series of other ponds was likewise visited for purposes of comparison. Mr. Congdon also acted as librarian of the laboratory, and considerable time was devoted by him to classifying and cataloguing

the now rather unwieldy collection of miscellaneous reprints.

Bradley M. Davis, Ph.D., past assistant professor of botany in Chicago University, finished during the summer the catalogue of the marine algæ, together with a section of the report dealing with the distribution of algæ and Zostera in the deeper waters of the bay and sound. Much of this manuscript had been written during the preceding spring, Dr. Davis having spent the months of April and May at the laboratory. The catalogue will contain more than 250 species of algæ, with records of their distribution and seasonal habits; and will include a list of the stations at which they were dredged. An introductory section on the general characteristics of the algal life of Buzzards Bay and Vineyard Sound has since been written, and the manuscript covering the botanical side of the survey is now practically complete, except for such editing as may be necessary to make the botanical and zoological portions conform in arrangement and style. An important part of the summer's work in botany was the completion of maps showing the distribution of 75 species of algæ which grow in the deeper waters of the bay and sound. It is expected that the most important of these maps will be published in connection with the catalogue, since they show, much more clearly than is possible in a mere description, the striking features in the distribution of the most characteristic species.

Donald W. Davis, professor of biology, Sweet Briar College, Sweet Briar, Va.—(1) *An Investigation of the Effects of Various Conditions acting at the Time of Impregnation upon the Size and Vigor of Fish Embryos.* For the time being, attention was restricted to the effects of various *temperatures,* and *Fundulus heteroclitus* was selected for experimentation because of its convenient spawning period. Each lot of eggs, taken from a single

female, was divided into equal parts. These parts were then fertilized by milt from a single male at temperatures differing from each other by 5°, 10°, 15° or 20° C. After a few minutes the two parts were again brought under identical conditions and so kept until hatching. At the expiration of a certain period, when practically all of the living embryos had hatched, all were fixed by the aceto-sublimate-formalin method, which was found to leave them well straightened. Careful records of mortality, rate of hatching, etc., in the different lots were kept. Measurements to be made upon the embryos, with a view to determining the tangible effects of such differences in treatment, are not yet complete. (2) A study of the alleged interference in branchial circulation resulting from the transfer of fishes from salt to fresh water, and *vice versa,* was also taken up. The conclusion of Bert and Mosso that such interference occurs in consequence of a clogging of the branchial capillaries by distorted blood corpuscles, was thought to be worth testing in view of recently published work by the director of the laboratory upon some other effects of changes in salinity. The common smooth dog-fish (*Mustelus canis*), the scup (*Stenotomus chrysops*) and the killifish (*Fundulus heteroclitus*) were experimented upon, the first two named being species which succumb quickly when transferred to fresh water, while the last named is commonly able to survive for some days in fresh water. The hypothetical clogging of the branchial vessels in these species was tested by passing physiological salt solution through the conus arteriosus at definite pressures, and the gills were then fixed for microscopical examination. Results immediately apparent revealed no such contrast as the statements of both Bert and Mosso would lead one to expect between fishes taken directly from salt water and those dying in fresh water. Further work will be necessary before a more definite statement of the results can be made.

Irving A. Field, professor of chemistry and biology, Western Maryland College, conducted experiments, to which allusion has already been made, with a view to testing the food value of certain hitherto unused marine animals. These were tested in respect to their palatability and digestibility by serving them, properly cooked, to numerous persons, who passed judgment on the quality of the food and the effects subsequently observed. Determinations of the chemical composition and nutritive value of the materials in question were, as has already been stated, undertaken by Dr. Alsberg. Various methods used commercially for the preservation of fisheries products (drying, salting, pickling, etc.) were applied to the forms studied. Statistics relating to the abundance of each species and the cost of preparing it for the market were also kept.

John H. Gerould, Ph.D., assistant professor of zoology, Dartmouth College, devoted a few days to the collection and study of a rare and hitherto undescribed species of sipunculid. Although two dredging trips were made with the *Fish Hawk* and the *Phalarope* for this express purpose, but a single specimen was obtained, which, however, was observed in a living condition, an opportunity which was regarded as of considerable value.

Charles W. Hargitt, Ph.D., professor of zoology, Syracuse University.—(1) *A Monographic Synopsis of the Anthozoa of the Region.* But little systematic attention has been devoted to the local representatives of this group since the work of Verrill and Smith more than thirty years ago. It has been the purpose of Dr. Hargitt to secure as full collections as the facilities at hand rendered possible, and to carefully review the group with reference to the species, their distribution, habits, development, etc. This work is now nearing completion so far as its laboratory phase is concerned, and will soon be ready for publication. At least one new species has been

found, and one or more have not as yet been identified with certainty. Some additional facts as to distribution and habits are likewise to be reported. (2) *Systematic Determinations of Local Cœlenterate Animals, as related to the Biological Survey now in Progress.* The survey has brought to light a number of new species of hydroids and medusæ, and a few hitherto quite unrepresented in the fauna of the region. Some account of these may be found in some recent "Notes on the Cœlenterate Fauna of Woods Hole."[7] Others remain to be determined. Dr. Hargitt accompanied many of the dredging expeditions made, and thus personally collected most of his specimens in the living state, as they came up in the dredge. Opportunity was thus afforded for obtaining data as to color, etc., which are of much importance in such determinations. (3) The manuscript of the catalogue of local fauna and flora, so far as this relates to the Cœlenterata, was criticized and revised as to nomenclature. (4) Some living specimens of the fresh-water medusa, Limnocodium, were received from the Bureau of Fisheries. A brief notice of these has already appeared in *Science* (November 8, 1907). A fuller account of this most interesting medusa is ready, and will appear in the near future.

George T. Hargitt, teacher of zoology, Syracuse (N. Y.) High School (now graduate student in Harvard).—*Studies of the Embryology of the Hydromedusæ.* The work on the embryology of the cœlenterates has been most often limited to two phases, viz., the place of origin of the germ cells and development of the medusa or gonophore; and the late cleavage of the egg, with the formation of the germ layers and the development of the planula and polyp. While attention has been so largely confined to the early cleavage and maturation of the egg, the results have been rather unsatisfactory and inconclusive, and often conflicting. The work under way is an

[7] *Biological Bulletin*, January, 1908.

attempt to supply the missing or less known phases of the early development of the cœlenterate egg, and especially that of the Hydromedusæ.

John D. Haseman, M.A., graduate student, University of Indiana.—*Studies of the Reactions of the Gastropod Litorina litorea to Stimuli.* Experiments were conducted, both in the laboratory and in the field, with a view to determining the conditions and stimuli which were responsible for the movements of these mollusks and the positions chosen by them. It is believed by the writer that Mr. Haseman has already prepared for publication a paper embodying the results of these studies.

William B. Herms, A.M., Ohio Wesleyan University (now fellow in zoology, Harvard University).—*A Comparative Study of Palæmonetes.* The habits, post-embryonic development and other facts in the natural history of the common local prawn, *Palæmonetes vulgaris*, were studied in relation to similar observations already made upon the related *Palæmonetes exilipes* of Lake Erie. Interesting points, both of similarity and of difference, were brought to light. A very close relationship between the two species undoubtedly exists. Several attempts were also made to acclimatize larvæ to higher and lower degrees of salinity.

William E. Kellicott, Ph.D., professor of biology, Woman's College, Baltimore.—*Biometric Studies of the Dog-fish* (*Mustelus canis*). The season was spent in the collection of data bearing on the general problems of correlation, growth, etc., in the dog-fish. A quite complete series of measurements, including about 30 characters, internal as well as external, was made upon about 300 individuals. Dr. Kellicott is at present working over these data and examining into the rate of increase in weight of the brain and viscera. Some interesting facts have revealed themselves, and it is believed that a paper embodying these will be ready in the near future.

Charles R. Knight, American Museum of Natural History, New York City, was engaged, as has been the case for several summers, in portraying pictorially some features of the local sea life. Mention may be made in particular of a tiger-shark (*Galeocerdo tigrinus*), and a dusky shark (*Carcharinus obscurus*). Of the latter, a specimen over ten feet in length was taken in the laboratory's fish trap, and was kept alive for a few days in the shark-pool belonging to the station. The lobster, blue crab and scup also received attention, a large canvas being devoted to a group of the last.

Edwin Linton, Ph.D., professor of biology, Washington and Jefferson College.—(1) Besides examining such fishes as were available among those taken in the fish trap of the Bureau in Buzzards Bay, a preliminary study was made of a large amount of material from fishes and fish-eating birds, collected during the preceding nine months by Mr. Vinal N. Edwards. In agreement with the experience of previous years was the fact that new habitats were found for species already known, and new or unrecorded species were added to the list of those previously known. Thus new species or new habitats were recorded for 21 species of fish. Adult specimens of *Tetrarhynchus bicolor* were encountered for the first time. They were found in the stomach of a dusky shark. Scoleces of this species had, however, been found in this and other hosts during previous years. The pigment which gives the characteristic color to the head and neck of this cestode was not dissolved by the killing fluid (chrom-acetic-formalin), and has not been decolorized by the alcohol in which the worms are preserved. (2) Of the pathological and diseased conditions which were noted, an interesting one is the case of an abnormal growth of the swim-bladder of a scup. This, when first seen, was a slender, white, vermiform object about two millimeters in diameter lying among the muscles of the side. It was at first thought to be a cestode, examples of which occa-

sionally penetrate the muscular tissue of their hosts. Upon tracing it forward, it proved to be a lateral prolongation of the anterior end of the swim bladder. At its origin it corresponded in structure to the swim bladder, but at its posterior (*i. e.,* distal) end it was rather firm and the walls were thickened. The alcoholic specimen, which has contracted somewhat, is 60 millimeters in length. (3) Butterfish were examined on five occasions for the flesh parasite described in the Bulletin of the Bureau of Fisheries.[8] The proportions of infected fishes were rather less than in previous years. (4) Considerable attention was given to the parasites of the puffer (*Spheroides maculatus*) with a view to preparing a special paper on the entozoa of that fish. (5) The preparation was begun of tables of the distribution of the parasites of fishes based upon collections made by Dr. Linton, at Beaufort, Bermuda, Tortugas and Woods Hole. These tables have since been completed and sent to the Bureau of Fisheries at Washington. (6) A beginning has also been made in the collecting of parasites from invertebrate hosts for the purpose of securing stages in the life history of those parasites of fishes whose early stages are found in invertebrates.

Albert J. May, A.M., instructor in the Boys' High School, Reading, Pa., made observations upon the medusæ of various local hydroids, and collected material for future study. *Corymorpha pendula,* which was especially sought for, on account of obscure facts in its life history, unfortunately proved to be very rare.

Hansford MacCurdy, Ph.D., professor of biology, Alma College, devoted most of his time to the study and tabulation of results obtained during the preceding summer relating to the hybridization of echinoderms.

William J. Moenkhaus, Ph.D., associate professor of physiology, University of Indiana, continued studies,

[8] Vol. 26, pp. 111–132.

begun some years ago, upon the hybridization of fishes belonging to widely separated genera and families. Such cross-fertilized eggs did not commonly hatch, or even develop far, but an interesting range of abnormalities was produced. A few experiments in cross-fertilizing certain invertebrates were likewise undertaken.

Raymond C. Osburn, Ph.D., instructor in zoology, Barnard College, Columbia University, was occupied chiefly in the preparation of a report upon the local marine bryozoa, basing this work for the most part upon collections made in the course of the biological survey during the past five summers. On account of the great abundance and almost universal distribution of many of these animals locally, the need of such a monograph has been much felt. Dr. Osburn has already found a considerable number of species which are new to the region, as well as discovering errors in the previous identification of certain common local forms.

Jacob Reighard, Ph.D., professor of zoology, University of Michigan, experimented upon certain features of the behavior of *Fundulus heteroclitus;* likewise compiled results obtained earlier in the summer at the Carnegie station at Tortugas, where experiments had been performed with the object of testing the alleged warning coloration of various brilliantly tinted tropical fishes.

Russell Richardson, graduate student in the University of Pennsylvania (now assistant in the department of comparative physiology, Harvard University).—*Response of Limulus Muscle to the Electric Current.* The two large lateral tail muscles were generally used. Both constant and interrupted (induced) currents were employed; and the stimulus was applied either by wires or by nonpolarizable electrodes. Endeavor was made to find out whether there was more than one form of curve to be derived from induced shocks, as had been found by some

workers; but all such attempts gave negative results, only one form of curve being obtained. The contraction is very rapid, and the height of the curve varies, within certain limits, as the strength of the stimulus. The relaxation is rapid at first, but later takes place more slowly. Summation is more or less regular. With constant current there were generally obtained the usual stimulations at the make and break of the circuit. The form of the curves varied greatly, however, according to the direction in which the current traversed the muscle. The weak constant current caused a marked relaxation of the muscle, only when passing through it in an ascending direction. Fatigue in Limulus seems more or less regular. As it progresses, there is a noticeably greater interval between the contraction and the relaxation. The latter also becomes much slower. After this stage, the height of contraction gradually diminishes until no response at all is obtained.

George G. Scott, A.M., instructor in biology, College of the City of New York.—(1) *The Effect of Poisons, at Different Temperatures, on Fundulus heteroclitus.* Sixteen experiments are recorded. In each case two lots of fish were used, one lot being kept at the temperature of the laboratory, *i. e.,* about 70° F., while the other lot was kept at a lower temperature, *i. e.,* about 50° F. Different dilute solutions of a variety of organic and inorganic poisons were used. In eleven of these experiments it was distinctly shown that the effect of the poison was greater at the higher temperature; in four, the result showed no difference; while in one, the result was opposite to the first named effect. (2) *The Effect of Change in Density of the Water on the Blood of Fundulus heteroclitus.* It has been recently shown by Sumner that there may occur a passage of fluids into or out of the bodies of teleost fishes when the density of the medium to which they are accustomed has been sufficiently changed. This has been proved by demonstrating the occurrence of changes of

weight, and by other means. It seemed worth while to ascertain what effects, if any, such changes of water density have upon the blood. The results of a few typical experiments are here stated. Hæmacytometer determinations were made upon fishes subjected to different conditions. The mean blood count of a number of specimens of *Fundulus heteroclitus* in natural sea water was found to be 2,700,000 red corpuscles per cubic millimeter. Sea water contains about 3.5 per cent., by weight, of salts in solution. In an experiment in which the salt content of the water was increased to over 6 per cent. by the addition of sea-salt, the proportion of corpuscles had increased to about 3,500,000 per cubic millimeter. In the case of another lot of fishes which were placed in 1,500 cc. of sea water, to which 30 grams of sea-salt had been added, it was found after six hours that the number of corpuscles was 2,800,000 per cubic millimeter. In yet another lot which were placed in 1,500 c.c. of sea-water plus 60 grams of sea-salt, the blood count, at the end of six hours, gave 3,000,000 corpuscles. In a case in which 120 grams of sea-salt were added to 1,500 c.c. of sea-water the blood count gave 3,900,000 per cubic millimeter. A number of fishes were placed in sea water artificially strengthened to the point of containing about 9.5 per cent. of salts. After one hour it was found that the fishes had lost in weight, while the blood counts of two specimens averaged 2,800,000; at the end of two hours, a further loss in weight was noted in the remaining fishes, and in two specimens the average number of corpuscles counted was now 3,434,000 per cubic millimeter. Fishes which were placed in distilled water and subjected to the hæmacytometer test an hour and a half later yielded about 2,000,000 corpuscles to the cubic millimeter. In two experiments with distilled water there was at first a *decrease* in the number of corpuscles counted, then a gradual *increase* up to the normal, which increase later passed above the normal. The question as to whether or not the blood is diluted by the osmotic influx of water

can likewise be investigated by determining whether the freezing point of blood serum from a fish which has been kept in fresh water is higher than that of blood serum from a fish taken from its normal medium. Although experiments of this sort had already been performed by a number of competent investigators, it seemed worth while to make the test again. This was impossible to do in the case of Fundulus on account of the small amount of serum obtainable. The experiment was carried out, however, upon *Mustelus canis,* the "smooth dog-fish."[9] Five determinations were made with the blood serum of fishes taken from normal sea water, and five with blood serum of fishes that had been kept in fresh water for an hour. These experiments agreed in showing that the freezing point of serum from fishes kept in fresh water is much higher than that of fishes taken from sea water. It was thus demonstrated that the blood of fishes may be diluted by a sojourn in fresh water, and support is given to the view that the change in the number of corpuscles counted was due to dilution or concentration of the blood. The last mentioned experiment upon Fundulus, in which distilled water was used, suggests that after the first dilution of the blood, due to the physical process of osmosis, there occurred a physiological reaction on the part of the organism, the excess of water being expelled from the blood. That it remains in the body of the animal, however, is shown by the persistent increase in weight.

Francis B. Sumner, Ph.D., director U. S. Fisheries Laboratory, Woods Hole, Mass.—(1) The supervision of the *biological survey;* (2) experiments in the deaeration of the local salt-water supply; (3) an investigation into the meaning of the color variations of *Litorina palliata* Say (carried on jointly with James W. Underwood). The first two of these lines of investigation have already been discussed in the more general part of the paper; a

[9] The known physiological differences between elasmobranchs and teleosts can not, of course, be left out of consideration.

synopsis of the third has appeared in a recent issue of *Science*[10] and need not be repeated.

James W. Underwood, student and assistant in Olivet College, (1) assisted in the work of the biological survey, being occupied for some months in plotting out the distributions of the more frequent local species upon maps which had been printed for the purpose; (2) collected and studied the species comprising the local plankton during the spring season; (3) cooperated with the director in the above mentioned study of the color variations of *Litorina palliata.*

Ralph E. Wager, A.M., teacher of biology, state normal school, Potsdam, N. Y.—*Studies of the degenerative Changes in Hydroid Polyps under the Influence of Changed Polarity or Contact Stimuli.* Experiments were performed for the purpose of providing material in different stages of degeneration, with the object of subsequently studying not only the histology, but more particularly the cytology of the changes. Abundant material was at hand in the various species of Obelia, and a sufficient supply of the degenerating polyps was obtained to thoroughly test the killing and fixing methods, if not to satisfy the demands of the problem. Thereafter experiments were performed on Gonionemus for the purpose of obtaining regenerating tissues, with a similar intention of determining the cytological changes involved in their growth. Again a plentiful supply of material was available, and enough of the regenerating tissues was obtained to make possible a fairly thorough study.

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HEREDITY OF HAIR-FORM IN MAN

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The hair of man shows various morphological types. Between straight hair, on the one hand, and woolly hair, on the other, there are all degrees of closeness of spiral. For convenience three intermediate grades may be recognized; *wavy,* having a very slight or open spiral involving the entire hair from root to tip; *curly,* having a closer spiral involving the distal half of the hair; and *frizzy* or *kinky,* a close tight spiral of small diameter. Now, although the conditions thus named are not discontinuous, they stand for types that are fairly well appreciated and distinguished popularly, so that in a random lot of people practically all would place a given sort of hair in the same category.

These different types of hair form are associated with certain differences of the hair on cross section as well as in its method of growth. Thus straight hair is nearly circular on cross section, while in woolly hair the cross section is elliptical and the long axis is to the short as 100: 40 or 100: 50. In wavy hair the proportions are as 100: 60 or 70. The straight hair of the Japanese has the proportions of 100: 85.

Since the hair of most mammals is straight and nearly circular on cross section, we may regard this as the basal condition and the flattened hair as a specialized form marking an advance in the *differentiation* of axes. In addition to this difference in cross section hairs differ in the form of the hair follicle, which is in woolly hair not only flattened, but curved in an arc through a quarter of a circle. "Emerging from an incurvated mould, it can only

continue to roll up outside, given especially its flattened shape; it rolls up into a spiral the plane of which, at the beginning, is perpendicular to the surface of the skin" (Deniker '06, p. 43). As all gradations exist between straight hair and wool in other characters, so probably in the initial curvature. The intermediate nature of *waviness* is probably due to an intermediate degree of curvature beneath the skin. This curvature of the follicle, again, is a departure from the usual mammalian condition and is in the line of differentiation or advance.

We are now in a position to formulate our problem. How do the more specialized types of hair form—much flattened and much curved woolly hair and slightly flattened, slightly curved wavy hair behave in heredity toward each other and toward the nearly cylindrical straight hair?

The data for this study are derived from the same sources as those of our eye color study[1] and include the ancestral characteristics of about 500 children for two ascending generations. About 230 families are involved.

The nomenclature of hair form that collaborators were requested to employ was as follows: Straight, wavy, curly, kinky. As our cards were distributed only among whites the term "woolly" was not used. The terms seem to have been, for the most part, understood by the collaborators.

The first result revealed by an analysis of the pedigree data regarding hair form is that straight hair is recessive to the curved types. Thus to 70 pairs of parents both said to have straight hair were born 185 children of which we have records. Of these 167 are recorded as having straight hair; 13 "wavy" and 5 "curly." Also 164 grandparents, both with "straight hair," are said to have had 146 straight-haired children, 11 "wavy" and 7 "curly." Knowing how liable to slip collaborators are we venture to affirm that probably not less than 98 per cent. of the offspring of straight-haired parents have

[1] *Science*, N. S., XXVI, No. 670, pp. 589–592, November 1, 1907.

themselves straight hair.[2] The genuine cases of straight-haired parents producing wavy or curly hair in the children are probably cases of imperfect dominance—or heterozygotes in which the recessive type appears to dominate. In all such cases the grandparentage contains always one or more cases of wavy or curly hair. Cases of recessive heterozygotes are not rare in the experience of students of heredity. They do not invalidate the general idea of Mendelian dominance. Striking cases of all straight-haired offspring of straight-haired parents are seen in the Bal., Bea., Bri., But., Cla., Hof., Loe., Mil., Oat., Pot., Reg., Sam., Spr. and Whe. families, each of four or more children. In these families there are 63 children altogether, and all of them have straight hair.

A second criterion of Mendelism is found in crosses of the R $\times$ DR type where a recessive is mated to a heterozygous dominant; in this case expectation is fifty per cent. of each type. Eighty matings between straight and heterozygous wavy give 61 straight and 52 curved-haired offspring, and 22 matings between straight and curly give 53 straight and 38 curved; or altogether, 116 to 90 where 103 of each is expectation (Cf. Dou-B., Got., Halz., Kar., McBr. families). There is a slight excess of recessives, probably due in part to a tendency to designate as "straight" boys whose curly hair is cut short; possibly to some cases of failure to dominate.

A third criterion is found in the crosses of the DR $\times$ DR type where two heterozygotes are mated to-

[2] The principal sources of error in naming hair form made by our collaborators are as follows: (1) Citing in males the form of the short, clipped hair instead of the youthful *long hair.* Curly hair when cut short appears as straight hair; this source of error is great in the case of the grandfathers, who are frequently deceased; (2) recording a hair form from a hazy recollection; a slightly wavy hair is often recalled as "straight." An attempt was made to get a confirmation of all doubtful cases (*i. e.,* not in accordance with the law) and in almost all cases in which a reply was received one of the two "straight" parents of curved-haired children was found actually to have curved hair. One exceptional case is that of the Hil family, where three wavy haired children came from two straight haired parents. The mother probably has curly germ cells which fail to dominate.

gether. Expectation in this case is 25 per cent. of the straight hair and 75 per cent. of the curved types—of the later 25 per cent. being pure dominants (DD) and 50 per cent. DR. Of 59 offspring of two DR parents there were actually found 22 per cent. curly, 51 per cent. wavy and 27 per cent. straight, or 73 per cent. curved to 27 per cent. straight. This again accords closely with expectation and supports the view of the essential DR nature of wavy hair (Cf. Bar., Gav., Gen. families).

All results indicate with a high degree of probability that straight hair is recessive to spiral hair; but it is probable that the spiral form may, in some cases, fail to dominate.

We have now to consider the behavior of wavy in relation to curly or kinky, *i. e.,* the lesser grade toward the greater. The statistics show clearly that wavy hair is usually, if not always, a *heterozygous* condition, and not merely an intermediate stage that is recessive to a higher stage (curly) and dominant over a lower (straight). For straight by wavy frequently gives curly (10 per cent. of cases) as well as wavy and straight. The result is in close accord with the conclusion that wavy always carries both straight and curly germ cells and when mated with single yields in the offspring an equality of straight and curved hair. Thus 113 offspring of straight by wavy parents give 54 per cent. straight and 46 per cent. curved hair. The "curly" germ cell of a *wavy*-haired person, uniting with a "straight" germ cell, usually gives the heterozygous, wavy form; but in 23 per cent. of the cases fails to do so, owing, we may say, to the unusual activity of the curly determiner. Wavy appears also when the curly germ cells of a heterozygous *curly*-haired person unite with "straight" germ cells. As in the last case, the offspring are not all wavy; indeed, the proportion of wavy is less, for 53 per cent. of the offspring are *curly*. That peculiar strength which makes a heterozygote *curly* instead of wavy tends to make its heterozygous offspring also curly instead of wavy.

We can now formulate the results of this study in their relation to human marriage, combining them in part with those obtained by us for eye color. Two blue-eyed, straight-haired parents will have only blue-eyed, straight-haired children. Two wavy-haired parents may have straight, wavy- or curly-haired children but the chances for curly hair are slight. Two curly-haired parents may have children with either straight, wavy or curly hair and the proportion of curly-haired offspring will probably be large. When one parent has straight hair and the other curly hair the offspring will all have curly hair, if the curly-haired parent is homozygous—otherwise half of their children will have straight hair and half curved. But the families of straight and wavy haired parents will probably have straight as well as wavy and curly hair, for waviness is always heterozygous.

TABLE SHOWING INHERITANCE OF HAIR FORM IN ALL FAMILIES OF TWO OR MORE CHILDREN.

c, curly; s, straight; w, wavy; k, kinky. Letters in parentheses refer to *recessive* characters; when accompanied by a ? the recessive character is inferred. Brackets are employed to designate inferred gametic constitution. ?? implies doubt whether the assigned character is correct. — means no record.

Reference Letters.	Children.			Parents.	Nature of Mating.	Grandparents.		Expectation.		Remarks.
	C	W	S	Mother. Father.		Mother's Mother. Father's Mother.	Mother's Father. Father's Father.	Curved.	Straight.	
Bal			6	s s	R × R	s s	s c(s?)		6	
Bar	3	2	1	w[cs] c(s)	DR × DR	w[cs] s	s c	4.5	1.5	
Bea			5	s s	R × R	s —	s s		5	
Beh	1	6	1	w[cs] s	DR × R	c(s?) s	w[cs] s	4	4	Mother's sibs.: 1 c, 1 w, 2 s.
Bri			5	s s	R × R	s s	s s		5	
But			4	s s	R × R	s s	s s		4	
Byr	4	2		c(s) c	DR × D	s w[cs]	c c	6		
Cam	1	5	4	s w[cs]	R × DR	s s	s s??	5	5	
Cla			4	s s	R × R	s s	s s		4	
Dav			2	s s	R × R	s s	c(s?) s		2	
Deg		1	1	s c(s)	D × DR	s w[cs]	s s	1	1	
Dou-A		2	5	s c(s)	R × DR	w[cs] c	s s	3.5	3.5	
Dou-B	2		2	c(s) s	DR × R	w[cs] w[cs]	c s	2	2	
Dra	2			w[cs] k	DR × D	s c	s c	2		
Dru			2	s w[cs]	R × DR	w[cs] w[cs]	c(s?) —	1	1	
Elt	1	1	1	s c(s)	R × DR	s w[cs]	w[cs] s	1.5	1.5	
Eny		1	8	s w[cs]	R × DR	s s	w[cs] c	4.5	4.5	
Fal		1	6	c(s) s	DR × R	c s	s s	3.5	3.5	
Fis	2	1	1	w[cs] s	DR × R	w[cs] c(s)	c(s?) s	2	2	Mother's sibs.: 2 w, 1 s.
Fri			3	s s	R × R	s s	s s		3	
Fue			3	s s	R × R	s s	s s		3	
Gav	2	4	1	w[cs] w[cs]	DR × DR	w[cs] w[cs]	w[cs] w[cs]	5.3	1.7	
Gen		2	1	c(s) w[cs]	DR × DR	s s	w[cs] c	2.3	0.7	
Gla	2	1	4	c(s) c(s)	DR × DR	s c	c s	5.3	1.7	

TABLE SHOWING INHERITANCE OF HAIR FORM IN ALL FAMILIES OF TWO OR MORE CHILDREN.—*Continued.*

c, curly; s, straight; w, wavy. Letters in parentheses refer to *recessive* characters; when accompanied by a ? the recessive character is inferred. Brackets are employed to designate inferred gametic constitution. ?? implies doubt whether the assigned character is correct. — means no record.

Reference Letters.	Children. C	Children. W	Children. S	Parents. Mother. Father.	Nature of Mating.	Grandparents. Mother's Mother. Father's Mother.	Grandparents. Mother's Father. Father's Father.	Expectation. Curved.	Expectation. Straight.	Remarks.
Gor	2	3	6	w[cs] c(s)	DR × DR	s w[cs]	c c	8.2	2.8	
Got		2	2	s w[cs]	R × DR	c (s?) s	s w[cs]	2	2	
Gre		2		w[cs] w[cs]	DR × DR	s w	w[cs] w[cs]	1.5	0.5	
Hal_1	2	1	1	w[cs] s	DR × R	w[cs] s	s w[cs]	2	2	
Hal_2	2		2	s s??*	R × DR	s c	s s			*[Probably curly when grown long]
Har	3	1	6	c(s) s	DR × R	s s	s?? s	5	5	
Hil		3		s s	?DR × R	w[cs] s	s s	1.5	1.5	
Hof			5	s s	R × R	s s	c(s?) s		5	
Hop			2	s s	R × R	s s	s s		2	
Huf		2	1	w[cs] s	DR × R	s w[cs]	c s	1.5	1.5	
Hur		3	1	w[cs] s	DR × R	s s	c c	2	2	
Irw_1			2	s w[cs]	R × DR	s s	c w[cs]	1	1	
Irw_2		1	2	w[cs] s	DR × R	— —	— —	1.5	1.5	
Jem	2	1		w[cs] s	DR × R	s w	s?? s	1.5	1.5	
Ker	1	1	2	w[cs] s	DR × R	s s	w[cs] s	2	2	
Koc	1		4	s s??*		s w[cs]	s s			*[Probably curly when grown long]
Lat	4		1	c(s) s	DR × R	c s	s s	2.5	2.5	
Loc_1			5	s c(s)	R × DR	s c(s?)	s c	2.5	2.5	
Loc_2			2	w[cs] s	DR × R	c s	w[cs] c(s?)	1	1	
Loe			4	s s	R × R	s s	c(s?) s		4	
McBr	2		3	s c(s)	R × DR	c s	s c	2.5	2.5	
Mea	1	2	1	s s??*		c(s) c	s s			*[Probably curly when grown long]
Mil_1			3	s s	R × R	s s	s s		3	
Mil_2			6	s s	R × R	s s	s s		6	

TABLE SHOWING INHERITANCE OF HAIR FORM IN ALL FAMILIES OF TWO OR MORE CHILDREN.—*Continued.*

c, curly; s, straight; w, wavy. Letters in parentheses refer to *recessive* characters; when accompanied by a ? the recessive character is inferred. Brackets are employed to designate inferred gametic constitution. ?? implies doubt whether the assigned character is correct. — means no record.

Reference Letters.	Children.			Parents.	Nature of Mating.	Grandparents.		Expectation.		Remarks.
	C	W	S	Mother. Father.		Mother's Mother. Father's Mother.	Mother's Father. Father's Father.	Curved.	Straight.	
Moo			2	s c(s)	R × DR	w[cs] s	s s ??	1	1	
Mor			2	s w[cs]	R × DR	s —	c(s ?) —	1	1	
Mur-B	1		2	s* c(s)**	R × DR	s s	s ?? *** s ?? ***	1.5	1.5	* 1 sister has curly hair. ** s, in manhood, 1 sister has curly hair. *** Recollection hazy.
Oat			8	s s	R × R	— —	— —		8	
Pad		5		w[cs] w[cs]	DR × DR	w[cs] —	w[cs] —	3.8	1.2	
Poe			3	c(s) s	DR × R	s s	s* s	1.5	1.5	* Confirmed by letter.
Pot			4	s c(s?)	R × DR	s c(s?)	s c	2	2	
Pre	1	4	1	c(s) s	DR × R	c w[cs]	w[cs] s	3	3	
Rau			2	s s	R × R	w[cs] s	s s		2	
Reg			6	s w[cs]	R × DR	s s	s s	3	3	
Sam_1		1	1	s c(s?)	R × DR	w[cs] c	s c(s?)	1	1	
Sam_2		3	2	c(s) s	DR × R	w[cs] s	s s	2.5	2.5	
Sam_3			5	s s	R × R	s s	s s		5	
Sco	1		5	s s ??*		s c	s s			* [Probably curly when long.]
Sho			3	s s	R × R	s s	s s		3	
Spr			4	s s	R × R	— —	— —		4	
Sto-B			2	s s	R × R	s s	s s		2	
Swe			3	s s	R × R	s s	c(s?) s		3	
Tru	1	1	2	w[cs] s	DR × R	w[cs] w[cs]	s s	2	2	
Tuc	1	1		w[cs] w[cs]	DR × DR	c w[cs]	s w[cs]	1.5	0.5	
Voo			3	s s	R × R	s s	s s		3	
War-A	1	1		w[cs] w[cs]	DR × DR	c w[cs]	w[cs] s	1.5	0.5	
War-B			2	s s	R × R	c(s?) s	s s		2	
Web		2	5	s ?? s		c(s) s	s s			

Table showing Inheritance of Hair Form in all Families of Two or More Children.—*Continued.*

c, curly; s, straight; w, wavy. Letters in parentheses refer to *recessive* characters; when accompanied by a ? the recessive character is inferred. Brackets are employed to designate inferred gametic constitution. ?? implies doubt whether the assigned character is correct. — means no record.

Reference Letters.	Children. C	Children. W	Children. S	Parents. Mother. Father.	Nature of Mating.	Grandparents. Mother's Mother. Father's Mother.	Grandparents. Mother's Father. Father's Father.	Expectation. Curved.	Expectation. Straight.	Remarks.
				w[cs]		s	s?			
Wel		3	7	s	DR × R	—	c	5	5	
				s		s	s			
Wet			2	s	R × R	s	s		2	
				s		—	—			
Whe_1			6	s	R × R	—	—		6	
				c(s?)		—	—			
Whe_2		1	1	s	DR × R	s	s	1	1	
				s		s	s			
Wil_2			3	s	R × R	s	s		3	
				s		s	s			
Zim			2	s	R × R	s	s		2	
Total	110		202					123	189	

NOTES AND LITERATURE

ECHINODERMATA

Renewed Interest in Recent Crinoids.—Since the lamented death of Dr. P. H. Carpenter in 1891, the recent crinoids have received little attention as compared with the other classes of echinoderms. Aside from the obvious difficulty of securing material, this has been due to certain inherent difficulties which systematic work in this class affords. Carpenter and his successors have recognized but few genera, the largest of these being cosmopolitan in distribution, and the numerous species have appeared to be ill-defined and extremely variable. Consequently aside from A. Agassiz's great monograph on Calamocrinus, a few systematic papers by Hartlaub, Bell, Koehler, Döderlein and Chadwick, a monograph on *Antedon bifida,* by the last, and an important morphological paper, on arm-regeneration in Comatulids by Minckert, our knowledge of the recent crinoids, and particularly our understanding of the interrelationships of the subordinate groups, was, at the beginning of 1907, about where it was left by Carpenter nearly twenty years before. The cruise of the "Albatross" in the North Pacific in 1906 afforded one of her naturalists, Mr. Austin Hobart Clark, exceptional opportunities for the study of recent crinoids and recognizing the responsibility thus laid upon him, Mr. Clark has during the past year made numerous and important contributions to our knowledge.

His first paper, "Two New Crinoids from the North Pacific Ocean,"[1] gives a figure and description of a most remarkable new stalked crinoid, for which the name Phrynocrinus is proposed, and of a new species of Bathycrinus, a well-known deep-sea genus of stalked crinoids. So remarkable does Phrynocrinus appear to be that it is suggested a new family, "Phrynocrinidæ," be established for it. The characters of this family are unfortunately not suggested, and to one having only an indistinct idea of the characters upon which the already very large number of families (mostly extinct) of stalked crinoids is based, the proposal of a new family does not make a strong appeal.

On the same date, Mr. Clark published a paper on "A New

[1] *Proc. U. S. Nat. Mus.,* 32, pp. 507–512.

Species of Crinoid (*Ptilocrinus pinnatus*) from the Pacific Coast, with a Note on Bathycrinus,"[2] in which another remarkable genus of stalked crinoids is described and figured, and there is a discussion of some of the specific names used in Bathycrinus. The new genus is considered to be related to the interesting Calamocrinus which the "Albatross" collected some years ago near the Galapagos Islands.

A paper on "Crinoids of the Genus Eudiocrinus from Japan"[3] bears the same date as the two preceding. Eudiocrinus is a genus of free-swimming crinoids (comatulids) remarkable for having united radials, but only five arms. Two species were found to be common along the southern coast of Japan, and three specimens of a third, which is described as new, were also taken by the "Albatross." A summary of the genus, with a synonymy of its seven species and statements of the type-localities closes the paper. Two papers dealing with "New Species of Recent Unstalked Crinoids"[4] appeared in September and give us a little insight into the extraordinary wealth of material which the "Albatross" collected, for we have here descriptions of no less than 55 new species, of which 52 belong to the genus Antedon as used by previous writers. Mr. Clark points out that the commonly used generic name Actinometra is untenable, being a pure synonym of Lamarck's older name Comatula. As the free-swimming crinoids are now so commonly called comatulids, it is not an unwelcome discovery which thus rehabilitates Comatula. Free use is made of artificial keys in these papers, although their usefulness is impaired by their doubtless necessary limitation to the new species and two or three most nearly related forms. There is plain intimation that Carpenter's "groups" of the genus Antedon are not in all cases natural or satisfactory divisions and that a rearrangement of the species is necessary.

In his next paper, "New Genera of Recent Free Crinoids,"[5] Mr. Clark attacks this problem and shatters the old genus Antedon into eighteen fragments, entirely discarding the group arrangement of Carpenter. At first thought this seems like needlessly drastic treatment, but the more one studies Mr. Clark's reasons and results, the more satisfied one becomes that such treatment is unavoidable if we are to get at the true interrelation-

[2] *Proc. U. S. Nat. Mus.*, 32, pp. 551–554.

[3] *Proc. U. S. Nat. Mus.*, 32, pp. 569–574.

[4] *Proc. U. S. Nat. Mus.*, 33, pp. 69–84 and 127–156.

[5] *Smith. Misc. Coll.*, 50, pp. 343–364.

ships of the comatulids. Few zoologists realize how many species of recent comatulids are now known, and it may therefore be of interest to point out that while only four of the new genera proposed are monotypic, five have more than eighteen species each and one of these has over fifty. Mr. Clark's selection of new names for his genera is particularly to be commended, as all are derived from the Greek, terminate in *-metra,* and are euphemistic.

During the summer, Mr. Clark worked at the Museum of Comparative Zoölogy and some of the results of his work appeared in January in a paper, entitled "Notice of Some Crinoids in the Collection of the Museum of Comparative Zoölogy."[6] In addition to the description of eight new species, there is an important note on six-rayed crinoids, a key to the genus Bathycrinus in which eight species are recognized, a table showing the bathymetrical and geographical distribution of Bathycrinus, and finally a "Key to the genera of Antedonidæ." This key is an enlargement and slight rearrangement of the one published in October and includes two additional genera, both of which seem to be well-defined.

Not content with systematic work alone, Mr. Clark shows his interest in crinoid morphology, and the larger questions involved when the geological history of the class is considered, by a very important paper on "Infrabasals in Recent Genera of the Crinoid Family Pentacrinitidæ,"[7] in which he demonstrates, apparently beyond doubt, the presence of infrabasals in *Isocrinus decorus* and *Metacrinus rotundus.* As no less an authority than Carpenter himself "positively asserts that they do not exist in the recent Pentacrinitidæ," this discovery is very interesting.

Having found how heterogeneous a group the old genus Antedon is, Mr. Clark's attention was naturally turned next to the equally well-known genus Comatula, and the results are given in "The Crinoid Genus Comatula Lamarck; with a Note on the *Encrinus parræ* of Guérin."[8] It is interesting to know that Comatula is far more homogeneous than might have been expected and requires the coinage of no new generic names and the revival of only a single old one, Comaster. The latter however, includes 43 of the 50 species hitherto called Comatula (or Actinometra). The note on *Encrinus parræ* is important and interest-

[6] *Bull. M. C. Z.,* 51, pp. 233–248.

[7] *Proc. U. S. N. M.,* 33, pp. 671–676.

[8] *Proc. U. S. N. M.,* 33, pp. 683–688.

ing for it clearly shows that the familiar name *Pentacrinus mülleri,* which has been used for a well-known West Indian crinoid for over half a century must give way to the combination *Isocrinus parræ* (Guérin), the specific component of which antedates *mülleri* by over twenty years.

Although the genus Antedon of previous writers had already yielded him nineteen new genera, Mr. Clark's indefatigable labors convinced him that the residue left therein (some 36 species) was not a homogeneous or natural group. In his "New Genera of Unstalked Crinoids,"[9] he has analyzed it and resolved it into thirteen elements, three of which are monotypic and three contain only two species each. Although he names his new genera with his customary skill and euphony, and gives the genotype and other species of each, he does not tell us what is left for Antedon s. str., and if we attempt to figure it out for ourselves, we reach the remarkable conclusion that Antedon as now limited contains *minus* 7 species! For, in October Mr. Clark said that Antedon (in the restricted sense in which he then used the name) contained 36 species. Since October he has described two additional species, which would give him 38 species for the new genera described in April. But these 12 new genera contain a total of 45 species, and therefore Antedon s. str. must now have —7 species! Whether this discrepancy is due to the shifting of the limits of some of his earlier genera, or to species of other writers which he had previously overlooked, or to *nomina nuda* introduced in the paper under discussion, we shall leave to Mr. Clark to explain at some future time.—Besides his new genera of Antedonidæ, Mr. Clark splits Eudiocrinus into two genera which he considers fundamentally distinct, and he then proposes no less than *eight* families of comatulids, with 39 genera. As he gives no definitions, or even a key, to these families, we can not express an opinion as to their validity. We can only wonder if Mr. Clark's enthusiasm is not leading him to magnify relatively unimportant details into significant morphological differences, and blinding him to the fundamental similarities of structure which the Antedonidæ show.

The ten papers here reviewed are sufficient to convince any one that their writer is a worker of extraordinary industry and enthusiasm. More than this, however, they give promise that Mr. Clark is to become a worthy successor to Carpenter as an authority on recent crinoids. Situated where the great collections

[9] ***Proc. Biol. Soc. Wash.*, 21, pp. 125–136.**

of the National Museum, which, thanks to the "Albatross," probably contain the largest and finest lot of crinoids in the world, are constantly available, his opportunities are most unusual and it must be a source of pleasure and gratification to all students of echinoderms that he is living up to them so well. His work reveals unusual powers of analysis and of skill in making his distinctions tangible, as witness his artificial keys to genera and species which seem to be very usable. He is quick to see a new point in structure or a new interpretation of some point already known, and while he treats the work of Carpenter and other writers with the courtesy and consideration they deserve, he does not hesitate to point out errors or misinterpretations which they have made. If he possesses the necessary patience and persistence, there is every reason to believe that Mr. Clark's work will prove epoch-making in the history of crinoid morphology and taxonomy.

Two faults seem to the present reviewer to mar Mr. Clark's work so far, and it is greatly to be hoped that he will have the courage and self-control to eliminate them in the future. One is a tendency to rush into print on the discovery of each new fact or group of facts, and the consequent result is a multiplication of titles to afflict all future workers, and a decided weakening of the value of each of his papers. Had Mr. Clark made four papers out of the ten which have already appeared, not only would bibliographers have blessed him, but his work would at least seem to have more of the weight and dignity which its quality shows it to deserve.—The other fault is a far more serious one and appears to be the cause of whatever errors and ambiguities mar Mr. Clark's work. It is hastiness in reaching a conclusion, hastiness in grouping the conclusions reached and hastiness in preparing his results for the press. In a word, haste is Mr. Clark's besetting sin and threatens to be the source of much quite avoidable trouble. As an illustration of what is meant by this criticism, reference may be made to some points in Mr. Clark's paper, "New Genera of Unstalked Crinoids." In his introductory remarks, he corrects four or five slight errors in his earlier papers, all of which might fairly be said to have been caused by haste. Under Thaumatometra, "*Antedon ciliata* A. H. Clark, 1907 (=*Antedon tenuis* A. H. Clark, 1907)," is given as the genotype, but neither *ciliata* nor *tenuis* appear in the list of species referable to the genus. Moreover, if we go back a little we find that while *tenuis* and *ciliata* were described

in September, in October Mr. Clark substituted the name *stella* for *tenuis* as the latter is preoccupied. Now are we to understand that Mr. Clark has concluded his three names refer to a single species? If so the description of *tenuis* and *ciliata* as distinct species was, to say the least, hasty. Again, under Compsometra, we find the following bit of evidence of haste in preparation: certain characters "distinguish this species at once. The two species at present known are," etc. Evidently the first "species" should read "genus." Under Isometra, Mr. Clark says that the name *challengeri* which he bestowed on an Antedon in 1907 is a synonym because it was given "before its relation to *angustipinna* was detected." Under Pentametrocrinus attention is called to an important morphological feature of certain species of Eudiocrinus, which "seems to have escaped the notice of all subsequent workers," and yet Mr. Clark himself published, less than a year ago, quite a paper on Eudiocrinus, with description of a new species and an annotated list of all previously known ones. Finally, in concluding his paper, Mr. Clark says, "The genera of free crinoids belonging to the Comatulida may be grouped as follows," and he then gives eight families with their various genera. But we fail to find the Atelecrinidæ or the genus Atelecrinus mentioned, and we can only guess whether the genus is considered synonymous with one of those given (which hardly seems possible) or is omitted through carelessness. Now while it is true that none of these slips is serious, Mr. Clark has not hesitated to criticize other writers for very similar blunders, and their presence in his work necessarily affects our estimate of its reliability. It is of the greatest importance, if the mantle of Carpenter is to rest becomingly on his shoulders, that in his future work, Mr. Clark reveal a greater patience, a more controlled enthusiasm and a more painstaking care in the preparation of his results for publication.

H. L. C.

ANIMAL BEHAVIOR.

Recent Work on the Behavior of Higher Animals.—The members of the genus Mus—the rats and mice—seem in a fair way to become the classic animals for comparative psychology, as the frog has long been for physiology. The work of the Harvard school, examined in our last review, dealt largely with these animals. The recent work of the Chicago laboratory is concentrated even more precisely on the white rat.

In his earlier work on "Animal Education," Watson had made such a general study of the behavior of the white rat as to give a survey of the problems and methods for future work. He and his collaborators have now undertaken a well-considered campaign of intensive investigation in the different phases of the rat's behavior.

The matter selected for first attack is "the determination of the relative importance of the several sensations of a given animal in its adjustment to its environment." What senses does the rat use in finding its way about and what part does each sense play? To this is devoted the main recent work from the Chicago laboratory.[1]

Watson finds, as Yerkes did with the dancing mouse, that the rat makes comparatively little use of senses that we are accustomed to think of as the all-important ones. His conclusion that sight, touch, hearing and smell play little, if any, part in the rat's finding its way about may almost receive the usual reportorial characterization of scientific results as "startling."

The method of work was to place the rat at the entrance of the complicated "Hampton Court" maze, with its many passageways and blind alleys, and allow it to find its way to the central compartment, where food had been placed. This was repeated many times, till the correct path was completely learned; many different rats were used, and a thorough study was made of the rat's method of finding its way. The questions are essentially, (1) what senses does the rat use in learning the correct path; (2) what senses does it use in following the correct path after it is learned?

To answer these questions, one or more senses were excluded, in different specimens, either by operative procedure or by other methods. The following extraordinary results were reached:

1. Blinded rats, or those studied in complete darkness, learn the path as quickly and follow it as readily as do those that can see. Even if the path is learned in the light, blindness causes no disturbance in later following it. (One rat formed an exception, finding its way in the dark only with the greatest difficulty.)

2. Rats deprived of smell and of hearing do not differ from normal ones in learning and following the correct path. This is true even when these rats *are likewise blinded.*

[1] Watson, J. B. Kinæsthetic and Organic Sensations: their Rôle in the Reactions of the White Rat to the Maze. *The Psychological Review*, Monograph Supplement, Vol. 8, No. 2, 1907, 100 pages.

3. Removal of the long vibrissæ or "feelers" on the face at first disturbed the rats greatly. But if, before testing them with the maze, the rats were allowed forty-eight hours to become accustomed to the loss of the vibrissæ, then they threaded the maze as readily as did normal rats. This was true even if these same rats were blind or without smell.

4. Altering the temperature conditions, changing the air currents in the maze, or making the feet insensitive does not disturb the rats, so that the corresponding senses seem to play no part in the behavior.

5. The evidence is strong that taste plays no part in the matter.

Apparently then we can exclude sight, touch, smell, hearing, taste and the temperature sense as factors of any importance in finding the way through the labyrinth. How then *does* the rat find its way?

Evidently the rat relies for its guidance mainly on the complex of inner sensations due to its own movements, the amount of effort it has put forth, and the like; the "kinæsthetic and organic sensations." In threading the maze, the animal learns how much effort it is to put forth going in a certain direction, which way and how much it is then to turn, how much effort to put forth in the new direction, which way to turn again, etc. It finally knows the entire path as a combination of such efforts and turns. The behavior of the rat is somewhat like that of a person who may, in the dark, walk about a house with which he is familiar, threading his way among tables and chairs, without touching them. But in man this involves many memory images of the various objects and their relative positions and distances. In the rat such images evidently play little if any part; it is mainly a matter of amount of effort, direction of turn, and the like. Watson is inclined to conclude that the rat has no such images; that the purely intraorganic sensations account for the entire behavior; that the rat uses in threading the maze no sense data from the outside, either past or present.

If this is true, then if the trained rat could be started at the entrance of the maze so as to get the proper "cue" at the beginning, and then *the entire maze lifted from the floor, so as to leave a clear space to the food in the center, the rat ought nevertheless to follow the same complex path that it follows when the walls of the maze are present.* Would this occur? Could not the experiment be tried?

While it appears conceivable that the running of the maze, after it is learned could be exclusively a matter of the inner sensations, so that the rat might follow the path even if the maze were absent, it is extremely difficult to see how this could be the case with the first learning of the maze. Our proposed experiment of removing all source of "extraorganic" sensation by doing away with the walls of the maze seems a *reductio ad absurdum;* the rat certainly would not learn the typical maze path under such conditions. How does the rat *learn* that it must put forth so much effort in a certain direction, then turn in a certain way? It would seem that for this, certain data from outside,—due either to feeling the wall with vibrissæ, or running squarely against it, or the like—are necessary. Even when the rat runs full tilt against a wall, that gives some sort of an extrinsic sensation that would seem to require consideration.

This is a point which the author does not make clear, though he seems to argue decidedly that it is possible to explain the entire behavior, both in learning and in finding the way after it has been learned, from the purely inner sensations. Does he perhaps hold that the only effect sensed by the rat, when it runs against a wall, is one of restraint, of prevention of further effort in that direction? Such a view would seem possible, if at all, only for actual collision at full speed, while cases where the rat merely feels the wall with its vibrissæ seem hardly open to this interpretation. It would have been helpful to certain readers if the author had so far recognized their obtuseness as to take up this point explicitly. In passing it may be remarked that the entire paper is written in a curiously confused and careless manner, as if it were a first draft which the author had not found time to revise. So thorough and important an investigation deserved better treatment.

A further development of the work set forth in the paper of Watson is presented in a later paper by Carr and Watson.[2] If the rat's method of threading the maze is merely to go a certain distance (as measured by the amount of effort put forth) then to turn in a certain direction, etc., without any data from outside itself, then evidently it would be greatly disturbed by altering the lengths and proportions of the passageways. Or if it is set down not at the entrance to the maze, but in the middle

[2] Carr, Harvey, and Watson, J. B. Orientation in the White Rat. *Journ. Comp. Neurol. and Psychol.*, 1908, 18, 27–44.

of one of the passages, of course a different combination of movements will be required to reach the center; a combination which it will not have learned, so that confusion would result. On the other hand, if the rat recognizes the correct turns, etc., by sight or other extraorganic senses, then less confusion need result from the changes mentioned.

The paper of Carr and Watson is an account of the behavior of the rat when the alterations above mentioned are made. When the trained rat is placed, not at the entrance of the maze, but in one of the passages, it appears confused, wanders about, then suddenly gets a "cue," and runs directly along the correct pathway to the center. The authors argue that the animal gets this cue through the intraorganic sensations. The rat wanders till it finds that it puts forth a certain amount of effort in a certain direction and then turns in a certain direction, etc.; this combination is familiar, so that the correct movements for the rest of the course are at once "set off" by it.

When certain passages of the maze were lengthened or shortened after the animal had learned the correct path, this caused precisely such disturbances as would be expected if the kinesthetic sensations are the fundamental ones. If a passage is made shorter than before, the rat runs full tilt against its end, even though this would appear to be "in plain sight." If a passage is made longer, the rat tries to turn when it has gone the usual distance; it thus runs against the side wall. If a blind passage now opens at a distance corresponding to that of a former correct turn, the rat runs into the blind passage.

After many trials in the altered maze the rat finally learns to run through it as readily and correctly as before. This result is reached after many experiences of running into ends, "nosing" along side walls, trying to turn where there is no passageway, and the like. The reader is inclined to see here an excellent opportunity for study of the transformation of cues from outer sense data into kinesthetic cues. But again the authors argue that the whole is purely a matter of the inner sensations. If they would explain clearly just how the animal gets its kinesthetic cues without aid from outer sense data; how it learns without running into the end of a passage that it must put forth only so much energy in a certain direction; or if they would demonstrate that bumping into walls, nosing along passages, and the like, gives no extraorganic sensations of any consequence,

the reader would appreciate better their argument as to the *exclusive* rôle of the inner senses. One is slightly inclined to feel that the authors are making the common mistake of weakening the effect of a demonstration of the unsuspected great importance of a certain factor, by endeavoring to maintain that it is the *only* factor.

Another factor in rat behavior is dealt with in the paper of Slonaker.[3] Watson in his earlier work had found that young rats (25 to 30 days old) learn certain operations more quickly than do the adults, and this appeared to be due to the fact that the young were more active. They tried, in a short time, all sorts of movements, and were therefore likely to hit quickly upon the "right" ones. Slonaker makes a careful study of the comparative amounts of activity in rats of different ages, in order to see how far this is correlated with the quickness of learning. A revolving cage was used, of such a character that the activity of the rats was automatically recorded. One such experiment, with several rats, lasted 25 days; another 57; another 60. It was found that, while there are great differences in individuals, both the very young rats and the old ones (age about a year) were comparatively inactive; the period of greatest activity falls in the age between 87 and 120 days. No close relation was evident between these results and those of Watson on quickness in learning.

All together, the work of the Chicago laboratory has of late been directed with unusual precision on a well-defined single line of research. And hand in hand with this work on behavior have gone studies on the nervous system, growth and life history of the rat, many results of which have been published from the neurological laboratory. Such a unified and intensive series of investigations may well serve as a model of the best method for making solid and permanent advance in comparative psychology.

H. S. JENNINGS.

[3] Slonaker, J. R. The Normal Activity of the White Rat at Different Ages. *Journ. Comp. Neurol. and Psychol.*, 17, 1907, pp. 342–359.

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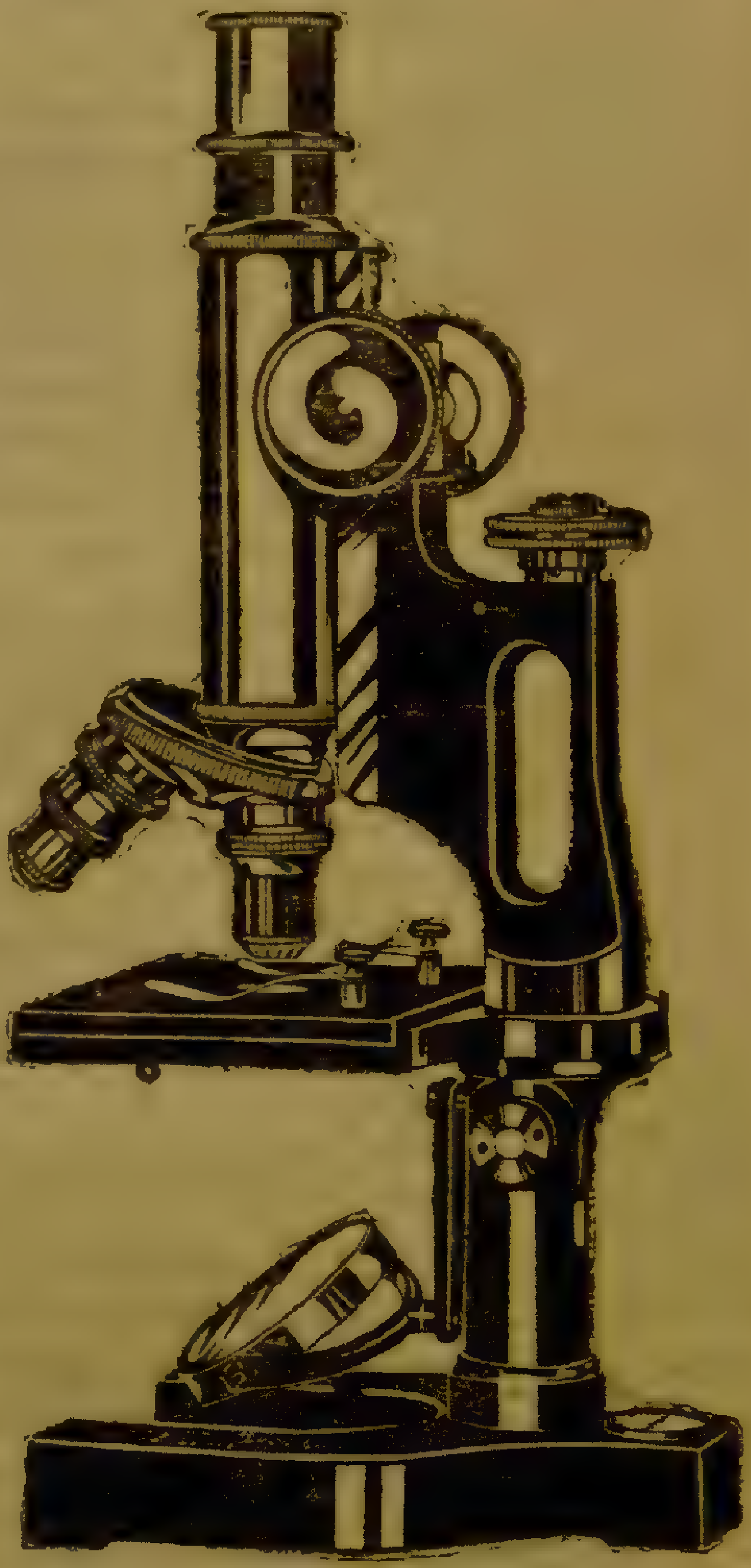

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Boston Society of Natural History,
Boston, Mass., U. S. A.

GLOVER M. ALLEN, *Secretary*

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THE ANCESTRY OF THE CAUDATE AMPHIBIA

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THE phylogeny of the group of vertebrates commonly called amphibians or batrachians has been, and still is to some extent, among the most obscure of the problems connected with the descent of animals. So far as I am aware there have been but few statements as to the possible ancestry of the Amphibia and no attempt has been made to set forth in detail the series of structures through which the animals have passed from the beginning of their line to the present. During the course of an extensive investigation on the extinct Amphibia of North America, the writer has reached some interesting conclusions in regard to the ancestry of at least one group of the modern Amphibia and these conclusions are here set forth in detail. Some of the facts offered in support of these conclusions have been given in other connections.

So far as at present known, the first trace of vertebrate life on earth is that of fishes in Ordovician rocks in Colorado and in two places in Wyoming, *i. e.*, the Black Hills and the Big Horn Mountains. In the Devonian, if the impressions from the Catskill are properly interpreted, the fishes had given rise to a quadrupedal type of animals which are usually known as the Amphibia. Only impressions of footprints in the sandstone are known, but these are quite instructive. There are no traces of the bones

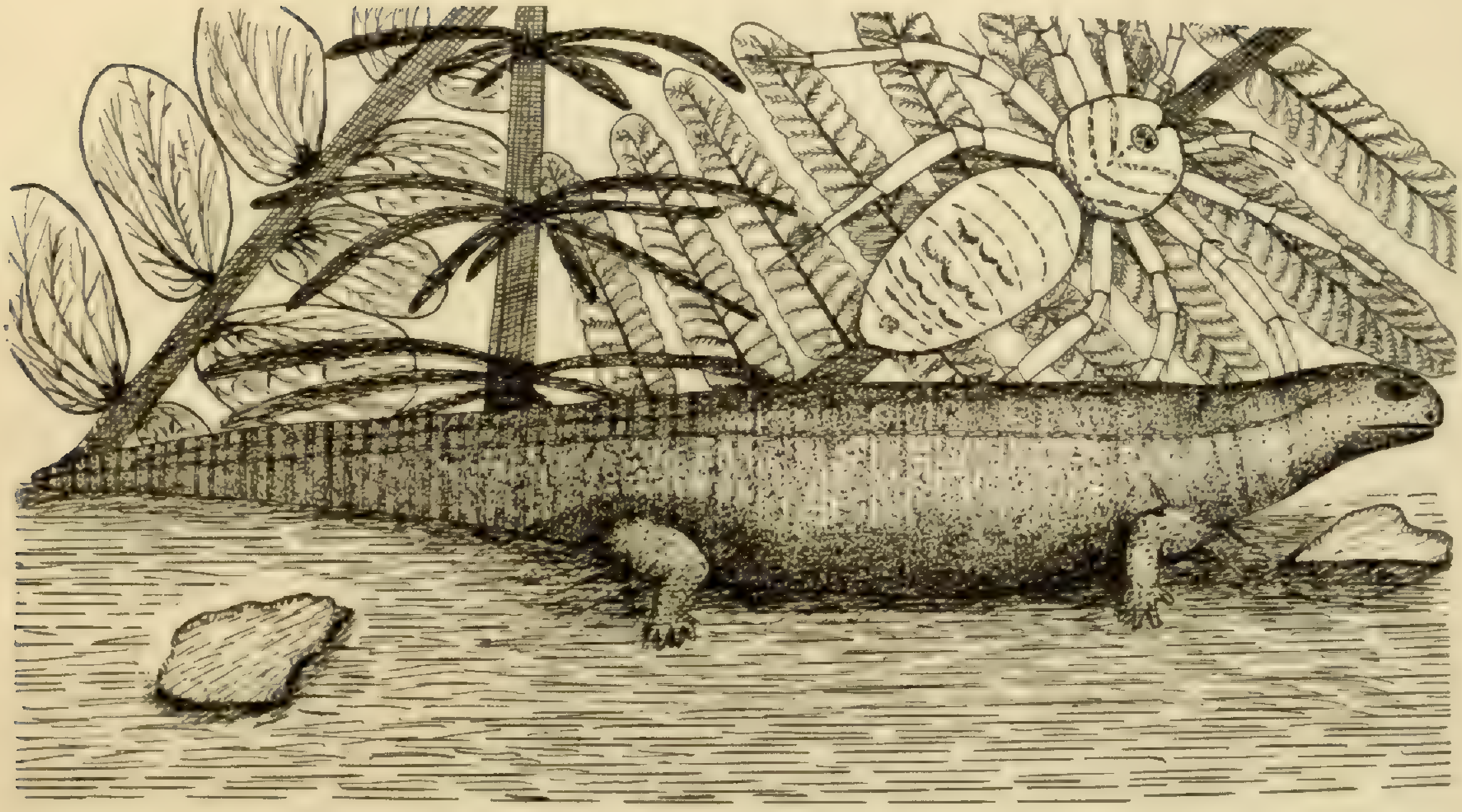

FIG. 1. Restoration of *Micrerpeton caudatum* Moodie from the Coal Measures of Illinois. Length of form, 49 mm. Spider is a composite restoration and is based on actual specimens and on the results of Roemer, Scudder, Beecher and Melander. $\times 2\frac{1}{3}$.

of these quadrupeds known in rocks of Devonian or of Mississippian age, although Lohest (1) some years ago called attention to some remains which he thought were amphibian from the Devonian rocks of France. Thevenin has recently cast doubt upon this interpretation by Lohest (2) and the figures as given by Lohest would seem not to be amphibian, but fish remains.

In rocks of the lower part of the Pennsylvanian occur, in North America, the first evidences of the bones of quadrupeds. The Amphibia show, even thus early, that their line had divided into three and possibly four distinct groups which are usually known as the Branchiosauria, the Microsauria, the Aistopoda and the Stereospondyli. The presence of the last group is indicated by the two vertebræ from the Carboniferous of Nova Scotia named by Professor Marsh *Eosaurus canadensis* and also by certain fragments of large ribs and large skulls from the coal beds of Ohio. The Temnospondyli did not make their appearance until the latter part of the Pennsylvanian, when their remains are found in Carboniferous rocks of Kansas, Illinois and Pennsylvania.

The Stereospondyli and the Temnospondyli are specialized side branches of the amphibian or reptilian stem and will not concern us further here. The Aistopoda are regarded by the writer at present as being specialized microsaurians. This would not favor the view of Wiedersheim as to the descent of the Cœcilians. This point needs further investigation and will be discussed elsewhere. The Microsauria Dr. Gadow has placed in the subclass Proreptiliæ and, in the opinion of the writer, his classification represents the correct facts, but further discussion will be postponed. The group to which the reader's attention is here invited is the one usually known as the Branchiosauria, representatives of which are found only in Western Europe and in North America, where a single specimen is known from Illinois. The group is a very small one both as to the size of the individual members and as to the number of species.

The Branchiosauria are distinguished from all of the other Amphibia-like vertebrates by the presence of short, heavy, straight ribs. The Microsauria always have long, thin, curved ribs. The Aistopoda usually are destitute of ribs or when present they are curved and slight. In conversation recently with Dr. Gadow he made the interesting suggestion that the characters presented by the ribs might be used as a basis on which to separate the group heretofore known as Stegocephala into two main divisions. One of the divisions would be the true Amphibia with the Branchiosauria as the representative order among the early forms, in which case the term Branchiosauria would be a misnomer, and the other Stegocephala would be included under some such name as the Pro-

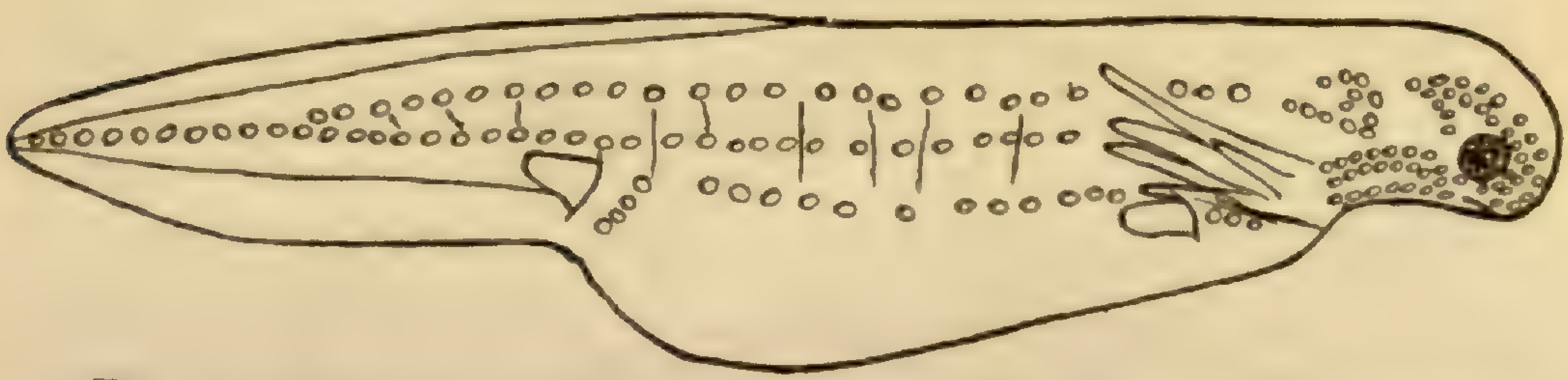

FIG. 2. Outline of a Larva of *Necturus*, showing the arrangement of the lateral line systems. After Platt.

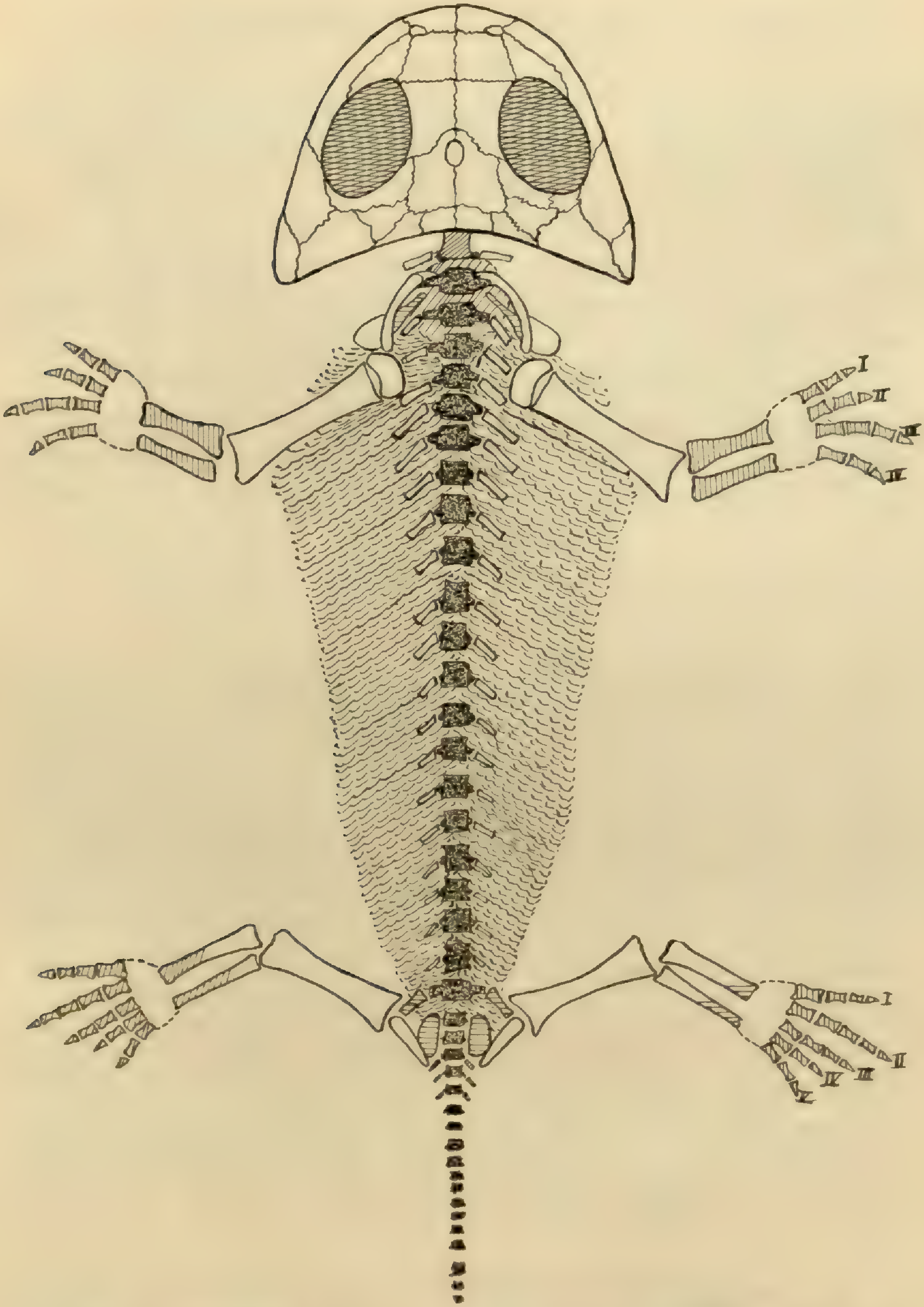

Fig. 3. Restoration of the Skeleton of *Micrerpeton caudatum* Moodie. The feet are conjectural and are based on the studies of Credner. The broad ventral armature is well developed in this form. × 3½.

reptilia or would be distributed among the reptiles proper. The former group is characterized by the short straight ribs borne on stout transverse processes and the

latter group is characterized by the long curved ribs borne intercentrally. There seem to be some difficulties in this classification, but it is hoped that they may be cleared up by future investigation.

The Branchiosauria, as has been several times suggested by various authors, represent the ancestral forms of at least the tailed division of the Amphibia. A suggestion as to the ancestry of the tailless forms will be given elsewhere. The conclusion that the Branchiosauria are the direct ancestral forms to the modern Caudata is based on several characters. These characters are: the structure of the skull, the structure and form of the vertebræ and ribs, the number of digits, the arrangement of the phalangeal elements, the characters of the pectoral and pelvic girdles, the character of the lateral line system, the structure and form of the long bones and finally the shape of the body; all of which will be discussed below.

It has been suggested on embryological grounds that the Amphibia are a degenerate group (3) and this is borne out, in so far as the Caudata are concerned, by a study of the cranium of the early and recent forms as well as by other structures. The cranium of the Branchiosauria is almost identical in structure with that of the Microsauria and it exhibits a completely roofed-over skull with only five openings, namely, those for the orbits, the nostrils and the pineal opening.

The elements forming the roof of the skull are quite constant in the Branchiosauria and also in the Microsauria and they differ only in position and relations. Practically the same elements form the skull roof in the two groups, but the forms differ in other important respects. In the skull of the Branchiosauria we find in the median line a row of elements in pairs, which extend the entire length of the skull. These are (beginning anteriorly): the premaxillæ, the nasals, the frontals, the parietals and the supraoccipitals. On the side of these elements lie others which vary in their position to some extent; the median elements are fixed and not so likely to

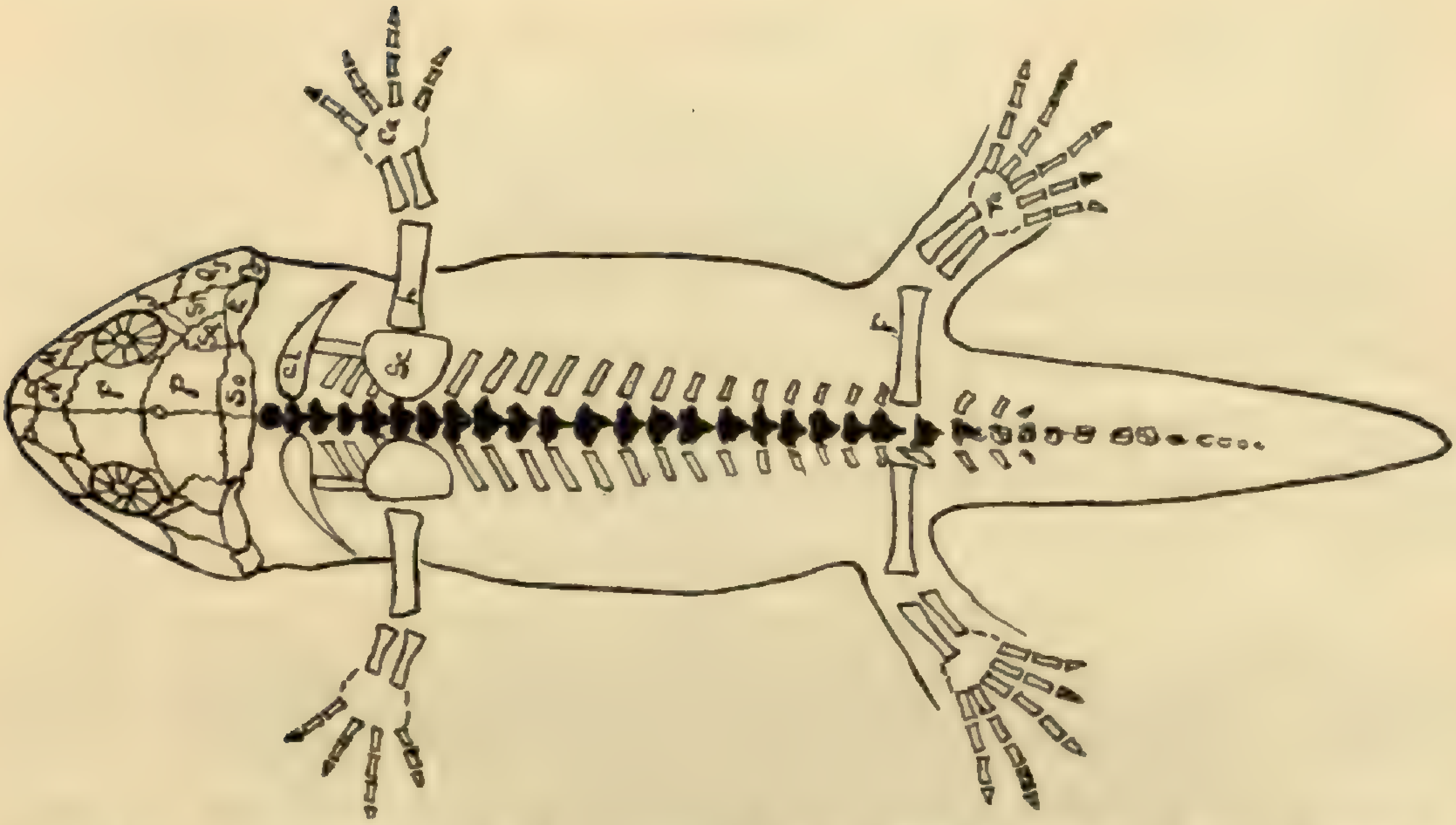

Fig. 4. Restoration with Outline of the *Branchiosaurus fayoli* Thevenin based on the figures given by Thevenin. The last phalanx in digit I of the hand is conjectural and the last two on digit II and the last one on digit IV of the foot are conjectural. From the Upper Carboniferous of France. ×2.

vary. Anterior to the orbit there are the prefrontal, the lachrymal, the maxilla, and lateral to the orbit lies the jugal. Posterior to the orbit lie the postorbital, the postfrontal, the squamosal, the supratemporal, the opiotic, and on the postero-lateral border of the skull lie the quadrato-jugal and quadrate.

In the skull of the modern Caudata we find an arrangement of the elements which is quite similar to that described for the Branchiosauria. In the skull of Megalobatrachus (Fig. 10), for instance, we find the following

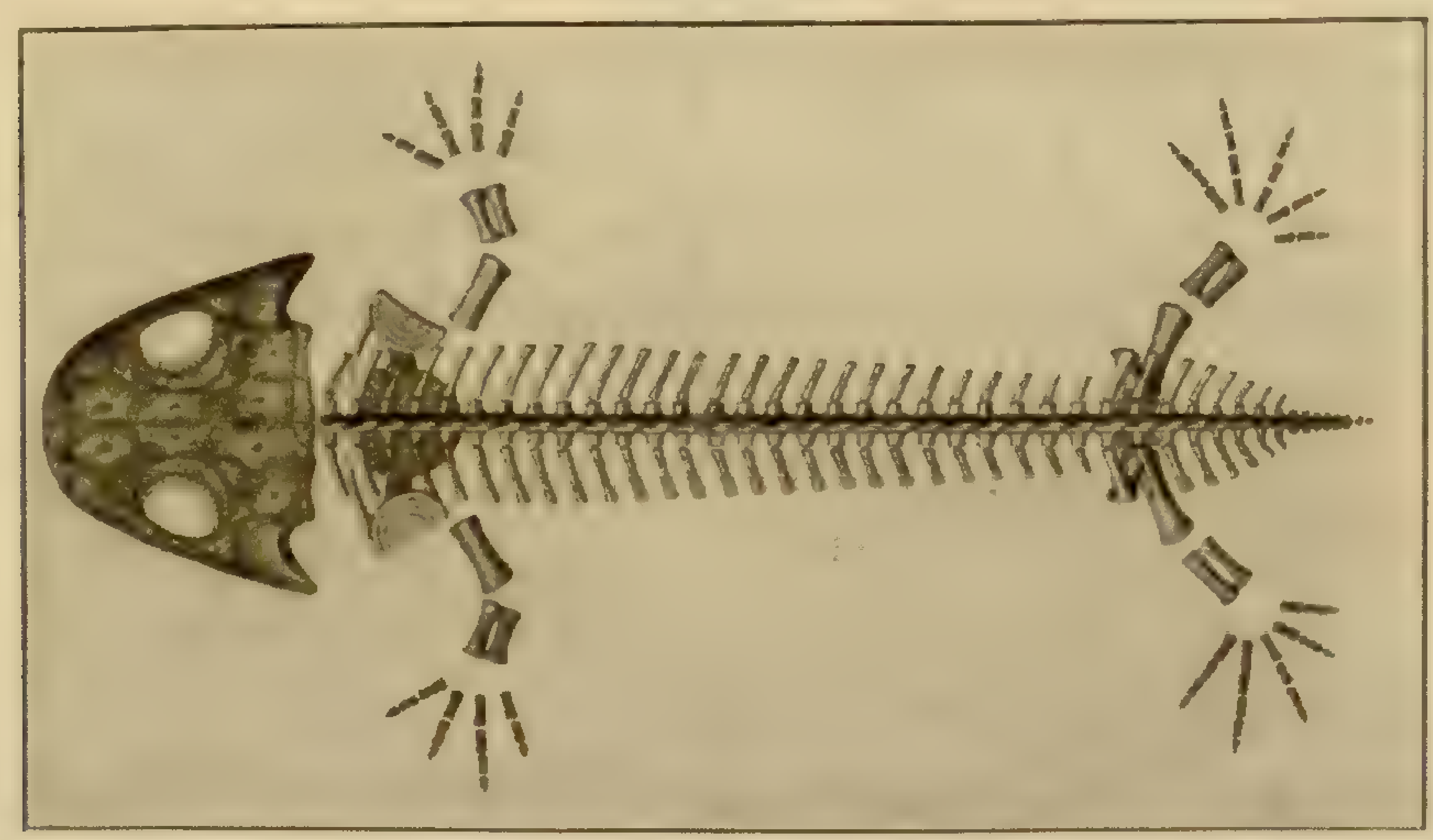

Fig. 5. Restoration of *Branchiosaurus amblystomus* Cred. from the Permian of Saxony. After Credner.

bones paired in the median line: the premaxillæ, the nasals, the frontals, the parietals, and on the posterior end of the skull occur the exoccipitals. In this series it is clear that the supraoccipital elements have disappeared. Lateral to the median paired row there are the maxilla, the prefrontal, the squamosal, and in allied forms the jugal, quadratojugal and quadrate. The epiotic is wanting in all skulls of modern amphibians except some coccidians and the elements are not so firmly united as in the skull of the Branchiosauria. The skull of the Caudata exhibits a weaker, more degenerate condition, than is found among the early forms. The lower surface of the skull is practically the same in the two groups, especially in the possession of a large parasphenoid. Teeth on the palate bones are lacking, for the most part, in the modern forms, which is another evidence of degeneracy.

If the structure of the vertebræ is now examined it will be seen that in this particular there is close affinity between the modern Caudata and the Paleozoic Branchiosauria. The vertebræ of the modern Caudata are amphicœlous and opisthocœlous, with the notochord rarely persistent and with the transverse processes springing off boldly from the body of the centrum. Similar conditions are observed in the Branchiosauria where the vertebræ, so far as they are known, are amphicœlous and the transverse process is unusually strong with the notochord probably persistent. The transverse processes give support to the short, heavy, stout ribs which lay in the flesh and made acute angles posteriorly with the vertebral column. The ribs in the Branchiosauria and in the later Caudata are indistinguishable so far as form is concerned. The point of difference is that in the modern forms the ribs are usually weaker posteriorly and are, for the most part, confined to the presacral region of the body. This is another instance in which the Caudata show their degenerate structure. On the basis of the ribs alone the Branchiosauria may well be separated from the Microsauria and from all other of the so-called Stegocephala, and would be considered as the true Amphibia,

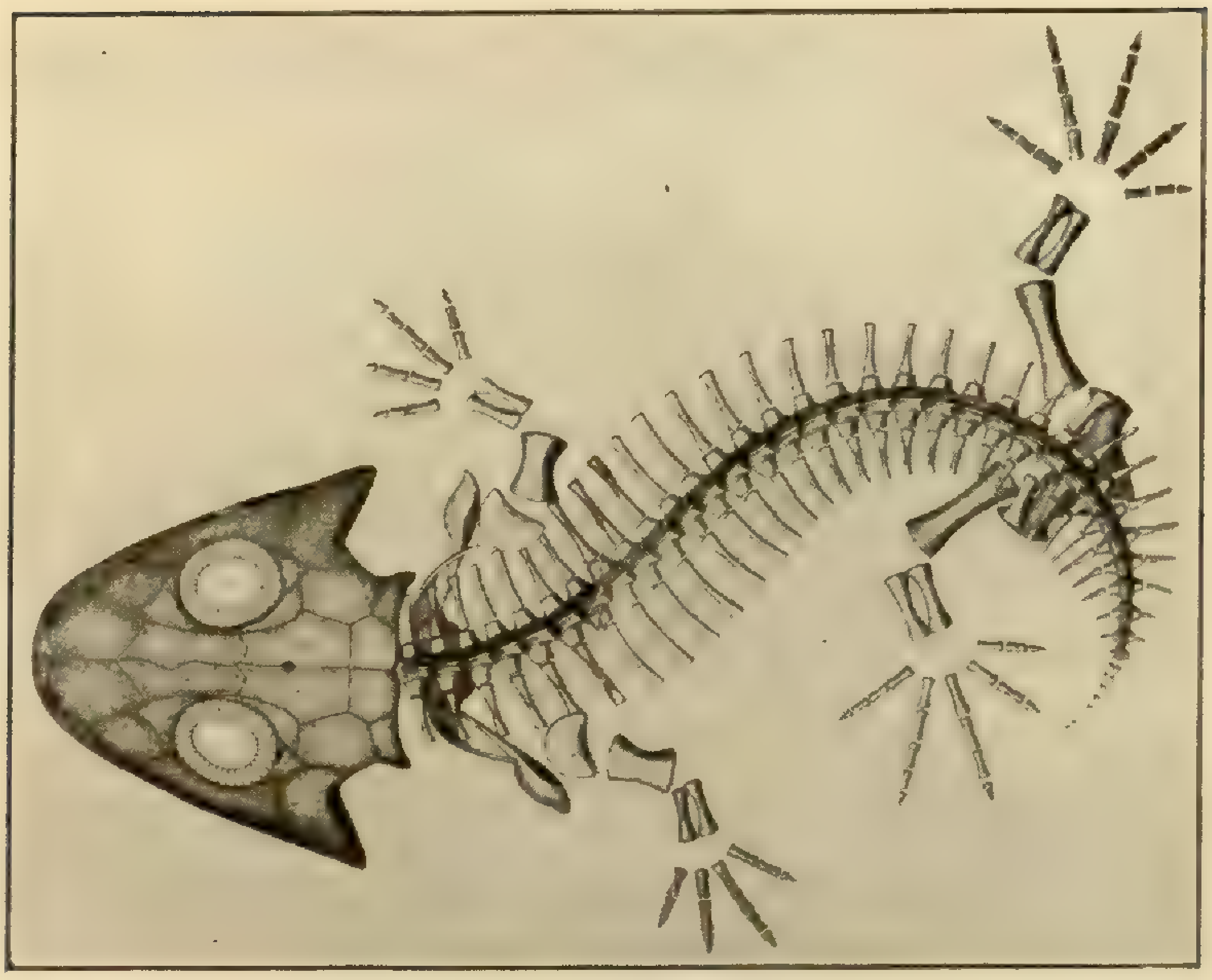

FIG. 6. Restoration of *Melanerpeton* from the Permian of Saxony. After Credner.

while all other forms would be excluded from this class and would have to be placed among the Reptilia, where they probably belong; whether they are to be considered as a subclass of the Reptilia or not, does not concern us here.

In the forelimb there are never more than four digits either in the Paleozoic Branchiosauria nor in the later Caudata. So far as I am aware, there is no paleontological evidence to show that there ever were more than four digits in the hand of the caudate Amphibia and in this discussion the first digit will be considered as No. I., the second digit as No. II. and so on. Fritsch, it is true, has figured five digits in the hand of *Branchiosaurus salamandroides* Fr. (Fig. 7), from the Permian of Bohemia, (4) but in giving us a glimpse into the material on which his restoration is based there are only four digits preserved in the hand, although Fritsch says the first had been lost. I doubt if there ever were more than four, and the digits in Fritsch's specimen were all preserved. In all of the Permian forms from Saxony Credner has figured four digits in the hand (Figs. 5–6).

The specimens recently described by Thevenin from the Upper Carboniferous of France (5) show only four

digits in the hand. In Fig. 4 a restoration of the *Branchiosaurus fayoli* Thevenin has been attempted. The reconstruction is based on the figures as given by Thevenin. Only one phalanx is restored and that is the distal one of the first digit. All of the rest were preserved. In the Wealden of Belgium the *Hylæobatrachus croyii* Dollo (Fig. 8) exhibits but four digits in the hand. In *Andrias scheuchzeri* Tschudi (Fig. 9) from the Miocene of Switzerland, there are but four digits in the hand, and in all of the modern caudate forms, so far as I am aware, there are but four digits and the phalangeal formula for all, both in Paleozoic and in later forms, is universally 3–3–4–3.

In the foot the Branchiosauria show the same agreement with the modern Caudata. There are always five digits and they usually have the phalangeal formula 4–5–4–3–3. Neither the carpus nor the tarsus is fully ossified in the Branchiosauria or in the later Caudata, although the carpus and tarsus are partly osseous in the Amblystomatidæ.

The pectoral girdle of the Branchiosauria consists usually of four elements, three paired and one unpaired. These are: the single interclavicle, the clavicles, the coracoids (cleithra?) and the scapulæ. Among the modern

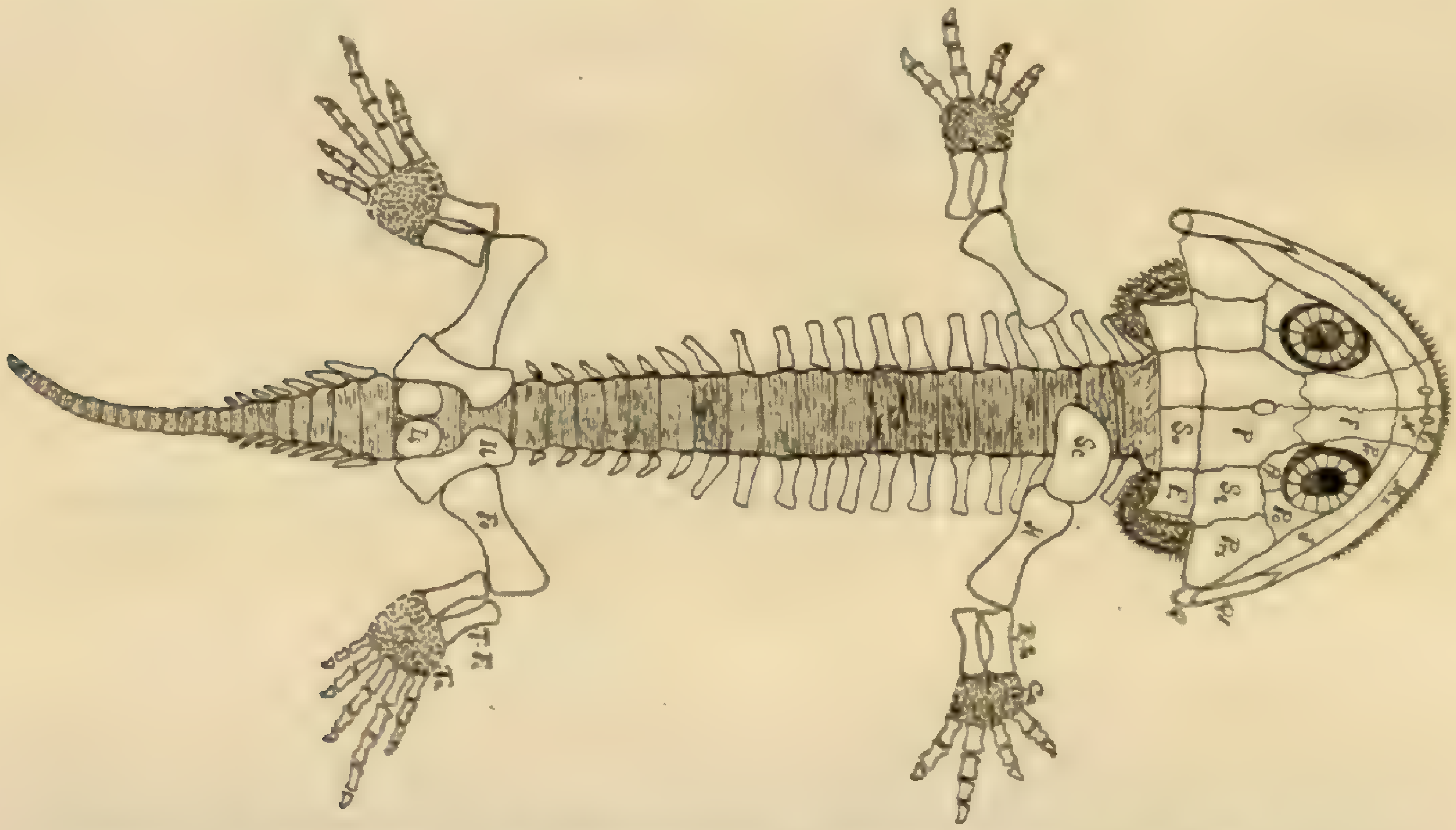

FIG. 7. Restoration of *Branchiosaurus salamandroides* Fr. from the Permian of Bohemia. Modified after Fritsch.

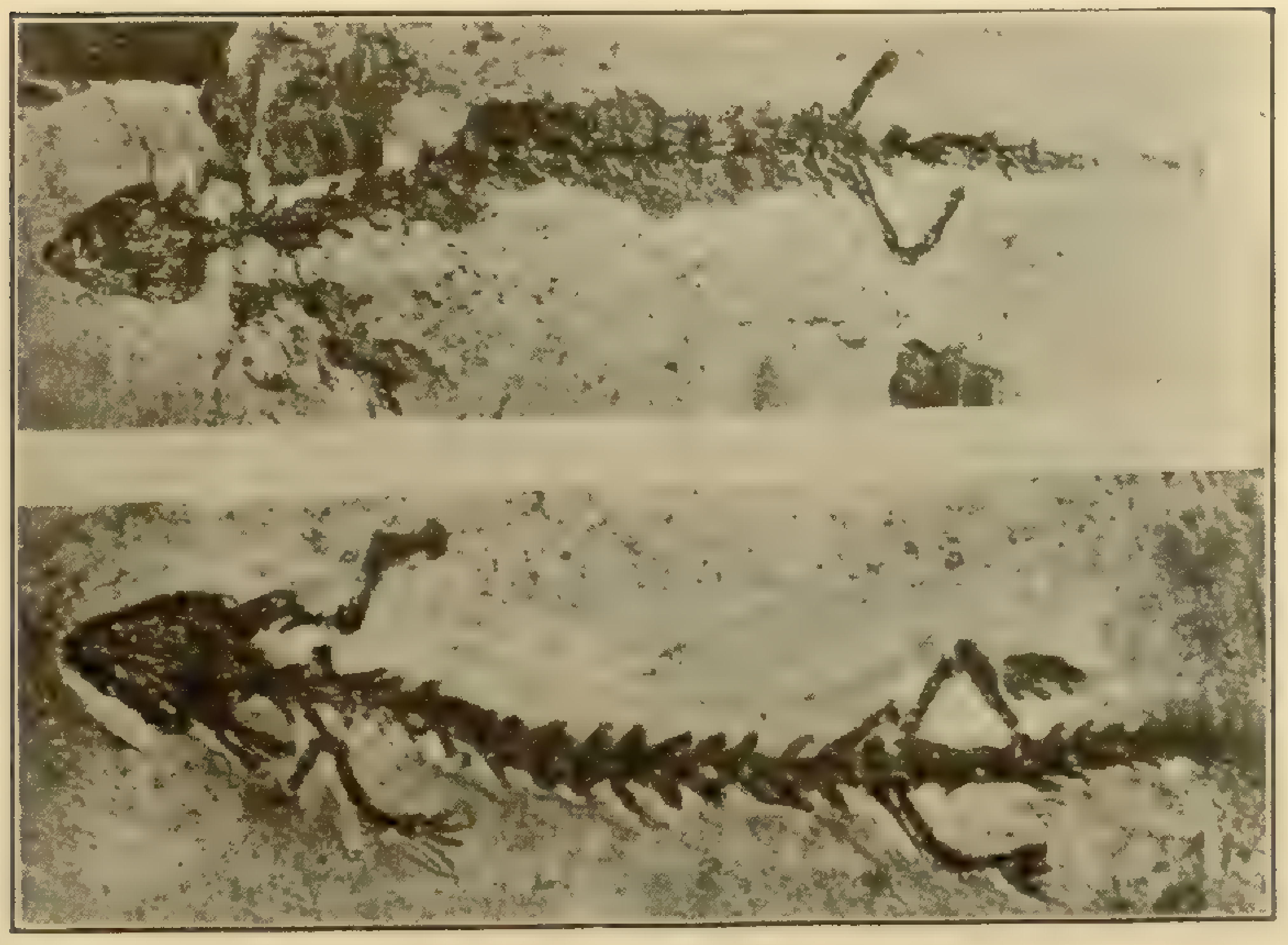

Fig. 8. *Hylæobatrachus croyii* Dollo from the Wealden of Bernissart. After Dollo.

caudate forms as well as among the Miocene forms all of the elements with the exception of the scapulæ have become cartilaginous, so that there remains in the modern caudate amphibians only a bony scapula. This seems to be the case in the Wealden Hylæobatrachus, but the single specimen is not well enough preserved to furnish definite information on this point. The pelvic girdle has, apparently, undergone no change in the evolution of the Caudata. The pubis is never ossified in either the Branchiosauria or in the latter Caudata and the ischium is usually plate-like, while the ilium is more or less rounded. The sacral rib, of which there is never more than one pair, is usually well developed.

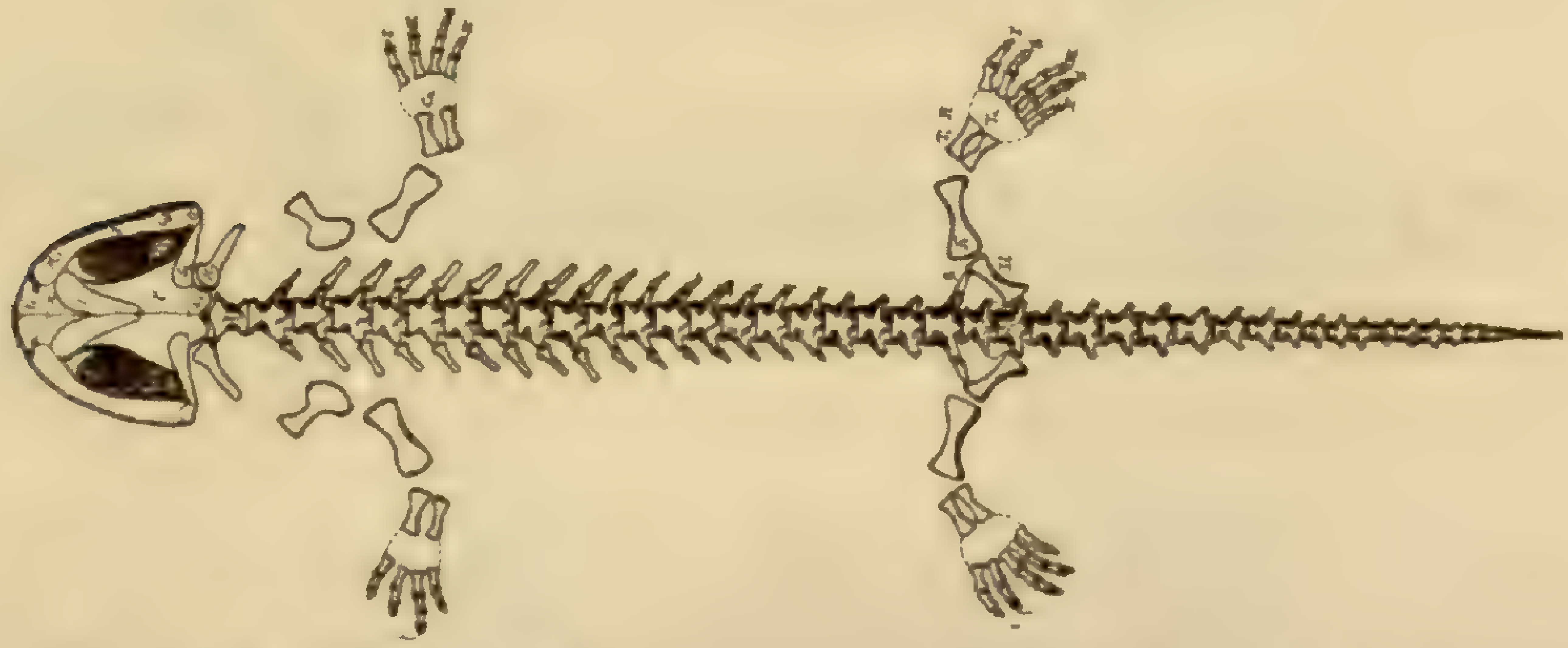

Fig. 9. Restoration of *Andrias scheuchzeri* Tschudi based on the drawings published by von Meyer in "Fauna der Vorwelt." × ¼.

In an essay now in press on "The Lateral Line Organs in Extinct Amphibia" the writer has called especial attention to the character of the lateral line organs as they are preserved in the single specimen of a branchiosaurian, Micrerpeton, from the Coal Measures of Illinois. A restoration of this form has been attempted in Fig. 1. The animal, as preserved, measures only 49 millimeters. It is apparently an adult, as there are no evidences of branchiæ and the limb bones are well formed. The spider shown in the restoration is a composite and is

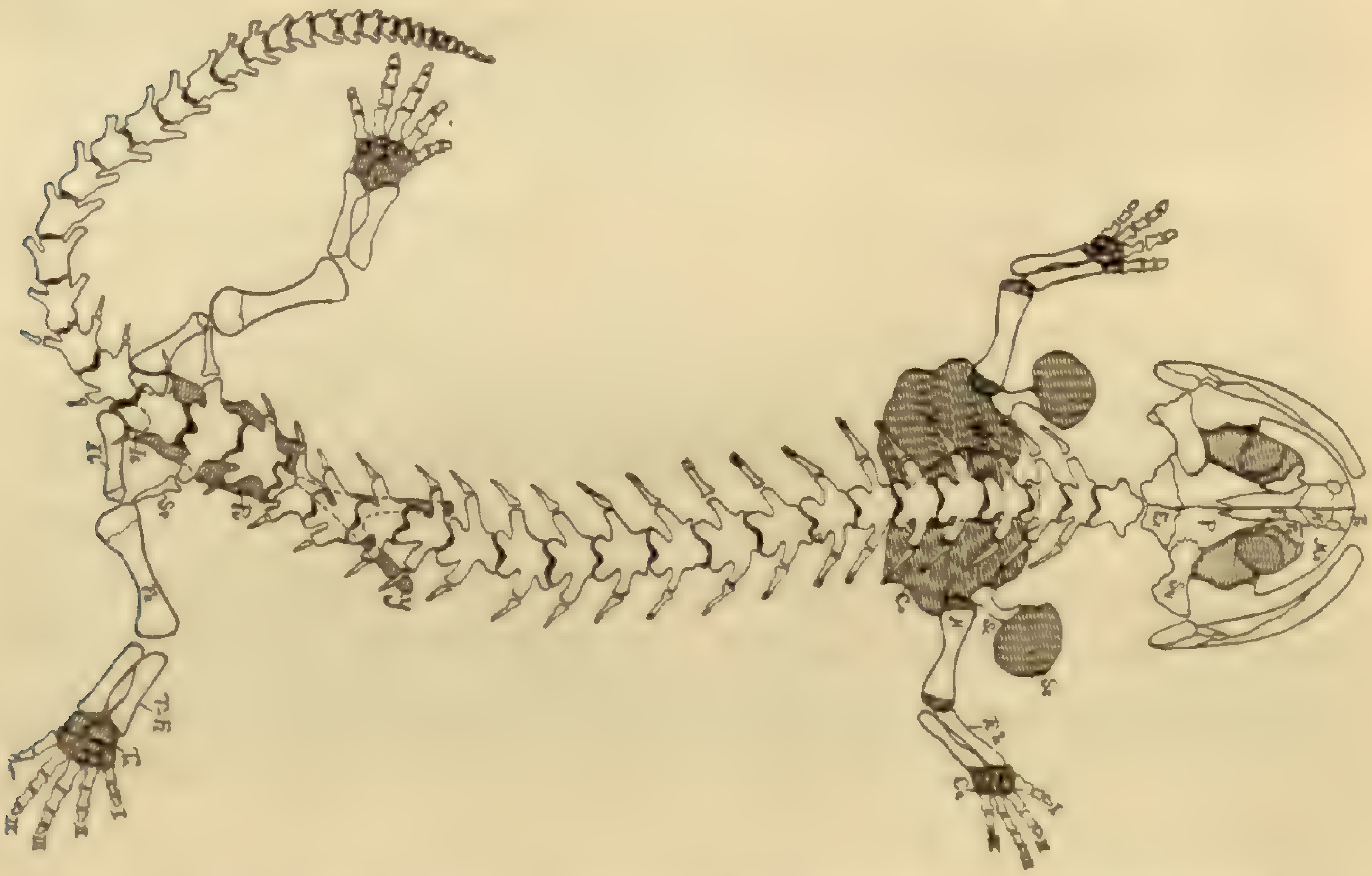

FIG. 10. The Skeleton of *Megalobatrachus japonicus* ——. After Osawa.

based partly on actual specimens partly on the results of Roemer, Beecher, Scudder and Melander. The body of the spider which was used as a model was about a half an inch in length. The particular characters in the amphibian which deserve mention now are the two lines representing the lateral line organs. There is seen a median lateral line which starts at the tip of the tail and runs forward. The other begins somewhat anteriorly and springs boldly from the median lateral line at a distance of a few millimeters from the tip of the tail. These lines represent rows of pigmented scales which show on the

specimen as dark lines. The sense organs were undoubtedly located beneath these specialized scales, much as the lateral line organs are protected in some of the fishes. In Necturus (Fig. 2) the arrangement of the lateral line organs is almost identical with what has just been described for Micrerpeton. I have suggested elsewhere that this similarity in the lateral line organs of these two forms may be indicative of relationship between the groups to which these forms belong. There is no reason why the type of lateral line should not have been preserved in the amphibians, since we know that in some of the fishes certain types of peculiar lateral line structure have persisted for nearly as great a length of time.

In the structure of the limb bones and ribs the Branchiosauria are much like the modern Amphibia in that the bones are formed almost entirely of perichondrium. There are never any bony epiphyses in any of the Amphibia. In some of the toads Parsons has seen the cartilaginous epiphyses calcified, but they are never osseous. The endochondrium is not at all or but slightly developed in the Amphibia, and in the fossilized bones this condition causes a concavity at the ends. In the Microsauria the endochondrium is more fully formed, although there are some in which the ends of the limb bones are nearly flat.

The form of the body in the Branchiosauria is strikingly salamandrine, as may be seen by referring to figures 1 and 4. In Micrerpeton the tail is quite long and almost equals the length of the presacral region. In the *Branchiosaurus fayoli* Thevenin (Fig. 4), the tail is shorter but the form is much the same. The body of the Branchiosaurus (Fig. 4) is more stout than that of the Micrerpeton (Fig. 3) and the ribs are longer.

In summing up all of the characters as presented by the Caudata and the Branchiosauria it seems most probable that the Caudata are but degenerate Branchiosaurians and the changes which have taken place in the skeleton are mostly brought about by the loss of certain parts.

Summary

1. The Stegocephala will probably have to be divided into two groups, one of which will be considered as Amphibia and the members of the other group will have to be placed among the Reptilia but can not all be placed under any single head since they represent divergent types and must be placed in with the reptilian groups to which they have probably given origin.

2. The Branchiosauria are the ancestral forms of at least the caudate Amphibia. The Branchiosauria are first known in the Pennsylvanian of North America and they present characters which separate them clearly from all other groups of the so-called Stegocephala.

3. The characters which the Branchiosauria have in common with the Caudata are: short, straight ribs; stout transverse processes springing from the body of the vertebra; practically the same number of presacral vertebræ; the same skull structure; the degenerate character of the pectoral girdle and the close correspondence of the pelvic girdle; the same number of the digits and the same phalangeal formula in the Branchiosauria and Caudata; the similar characters presented by the lateral line system; the structure of the long bones and the shape of the body.

4. There can be but little doubt that the Caudata are the direct descendants of the Branchiosauria, of which they are but degenerate forms.

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THE SPIROCHETES AND THEIR RELATIONSHIP TO OTHER ORGANISMS

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IN Ehrenberg's famous work, "Die Infusionstierchen als vollkommene Organismen," written in 1838, the fourth family of the Vibrionides, or vibrating animalcules, includes five genera which that author regarded as animals and distinguished as follows:

- Segmented threads (monad-stocks)
  - rectilinear (by rectangular transverse fission)
    - non-flexible .... *Bacterium*
    - serpentine and flexible .. *Vibrio*
  - spirally twisted (by oblique transverse fission)
    - twisted segments
      - flexible .... *Spirochæta*
      - inflexible
        - cylindrical elongate *Spirillum*
        - discoidal compressed *Spirodiscus*

The details of structure which Ehrenberg had elsewhere worked out with too imaginative industry, he sadly acknowledges are here "barred to our present powers of vision by virtue of their minuteness"; and he is forced to depend upon scanty data to differentiate the to him closely related genera. To-day three among the associated genera are generally recognized as bacteria and of the spirochetes alone is there doubt as to their proper relationship in the systematic tree.

However, Ehrenberg was not the first to observe such organisms. In 1773 O. F. Müller described corkscrew-like animalcules found in foul water, and in 1786 discussed and figured several species, unconscious that in 1777 Köhler had published the first figure of such a form.

[1] Studies from the Zoological Laboratory, The University of Nebraska, under the direction of Henry B. Ward. No. 90.

Yet both descriptions and figures are far too indefinite to permit of more than a guess as to the genus under consideration. Even Ehrenberg's work affords scanty means for the recognition of the forms of which he listed one spirochete and three spirilla. The group, though familiar to all students of microscopic life, has remained only superficially known up to very recent times, in fact until the discovery of the important rôle which certain of them play in the production of disease turned once more the attention of investigators in this direction. Despite the characteristic of flexibility noted by Ehrenberg, and the indifference they displayed towards ordinary methods of bacteriological culture, most authors have grouped these organisms together among the bacteria. Renewed attention to the group served to emphasize at once radical differences of opinion as to its interpretation.

Undoubtedly the impetus to this study was given by Schaudinn's discovery of such an organism in syphilis and the intuitive inference which has been abundantly verified that others would be found in similar relation to diseases as yet entirely unexplained. Working on this and on other species, Schaudinn confirmed the view of Ehrenberg as to the characteristic flexibility of the spirochetes, and determined the occurrence of longitudinal division and the presence of polar flagella, single save just before division. He also demonstrated certain differences between the form found in syphilis and other common spirochetes, which he thought served to justify their generic separation. Throughout he maintained firmly the animal nature of the group.

Almost simultaneously there appeared in 1906 several papers which dealt with the problem as to the nature of this group and arrived at diametrically opposite conclusions. In the first, by the parasitologist Blanchard (1906), was analyzed briefly the morphological basis for the genera of microorganisms in which the body has the form of a spiral. In comparison with these the author

considered very briefly also certain clearly bacterial forms (*Spirosoma, Vibrio, Spirobacillus*) and others distinctly flagellate (*Trypanosoma, Trypanoplasma*) which in his opinion manifest close relationship to the true spiral microorganisms of which he recognized three well-founded genera, *Spirillum, Spirochæta* and *Treponema.* The group of plant organisms he classed as follows:

Spirobacteria Cohn 1875

Bacteria more or less curved in a spiral, the curve forming at times only the arc of a circle, in other cases forming spiral coils more or less numerous. Organisms little flexible or not at all, multiplying by transverse division. Formation of endogenous spores demonstrated in a number of species.

Four genera: *Spirosoma, Vibrio, Spirobacillus, Spirillum.*

Of the last genus he says: *Spirillum* Ehrenberg 1830— Body spiral, cylindrical in transsection, not tapering at the ends. No undulating membrane. One or several flagella bent in a regular curve, either at both extremities or at one only. Formation of endogenous spores demonstrated in a number of species. Organisms relatively of considerable size, cultivated easily on various media used in bacteriology.

The spirilla are clearly bacteria. They live as saprophytes in wells, stagnant waters, the soil, liquid manure, etc., and generally in media very poorly oxygenated. Possibly one should include in this genus some forms which are found in pus, but it is doubtful if these play an active part in it, and up to the present time not a single species can be considered as surely pathogenic.

Over against these forms, and sharply contrasted with them Blanchard placed the animal organisms of a general spiral form. These he included in a single family, characterized thus:

Trypanosomidæ Doflein 1901

Flagellates twisted into a spiral, the coils being more or less numerous. Organisms flexible, with form more or less fixed, multiplying by longitudinal division. No endogenous spores. Locomotive apparatus consisting either simply of an undulating membrane, or of such a membrane together with one or two flagella. Not stained by Gram's method, not cultivated in the media used in bacteriology.

Four genera: *Spirochæta, Treponema, Trypanosoma, Trypanoplasma.*

The first two genera are very similar and include the only forms concerning the animal nature of which there is any question. It will be necessary to consider these somewhat closely. The first is characterized thus:

Spirochæta[1] Ehrenberg 1833

Body excessively slender, spiral, flattened, ectoplasm extending in a narrow undulating membrane which surrounds in a spiral the entire body. No flagella, no endogenous spores. Nucleus greatly elongated, filiform, in the axis of the body, with chromatin granules distributed along its surface. Reproduction in all probability by longitudinal division. None of the media used in bacteriology serve to maintain cultures of these organisms. Type species, *S. plicatilis.*

All these forms are by some students assigned to the bacteria. Some species are inhabitants of stagnant waters, others live in the sea or in decaying organic materials, while still others are parasitic. Among the latter are forms recently recognized as the cause of most virulent infective diseases in man and other animals. The genus characters given above are not in their original form, but as emended by Blanchard, and this emendation becomes now the basis of the group thus named. The emendation is based primarily upon the epoch-making investigations of Schaudinn.

[1] The name is often written *Spirochæte*, which does not conform to rules of Latin or of nomenclature.

Blanchard lists in this genus the following species:

1. *S. plicatilis* Ehrenberg 1833, from stagnant water.
2. *S. buccalis* Cohn 1875, from the buccal cavity.
3. *S. obermeieri* Cohn 1875, from the blood of man in cases of relapsing fever. The possible varieties of this species, found in various types of relapsing fever, are also noted.
4. *S. dentium* Koch 1877, very small species from the mouth.
5. *S. gigantea* Warming 1875, from brackish water.
6. *S. eberthi* (Kent 1880), from the intestine of birds.
7. *S. balbianii* (Certes 1882), from the intestine of lamellibranchs.
8. *S. anserina* Sakharov 1891, cause of septicemia in birds.
9. *S. theileri* (Laveran 1903), from blood of cattle.
10. *S. pyogenes* (Mezincescu 1904), from pus in a case of pyelitis.
11. *S. gallinarum* R. Blanchard 1905, cause of septicemia among chickens.
12. *S. refringens* Schaudinn 1905, from lesions of syphilis.
13. *S. pertenuis* Castellani 1905, from lesions of yaws.
14. *S. ovina* R. Blanchard 1906, from blood of sheep.
15. *S. vincenti* R. Blanchard 1906, from abscesses in man.

Also several other uncertain forms.

It is evident that this assemblage of forms is not entirely natural. Of many little is known beyond the size and manner of life. The latter presents radical differences, but the formation of new genera on purely physiological grounds is recognized as a most dangerous procedure. No doubt better knowledge, especially of the life cycles, will lead to the removal of groups of these species to new genera, but such must be based upon distinctive characteristics; any other method only results in greater confusion. New forms are being described constantly, *e. g., S. lymphatica,* which White and Proescher regard

as the cause of a lymphatic spirillosis; it stains like *Treponema pallidum.* More extended investigation alone will justify assigning a definite place to such organisms. Yet apparently the group of spirochetes producing relapsing fevers may justly be made an independent genus, even though their morphological differentiation is difficult. They constitute the newly created genus.

Spiroschaudinnia Sambon 1907

Blood parasites only imperfectly known. In blood of vertebrate host, they appear as minute, wavy or spiral threadlike bodies. With undulating membrane but no flagella. Free stage alternates with intracellular resting stage with parasite coiled up in host cell. Sporogony in ticks. Stages have been demonstrated in ova, showing the hereditary transmission of the infection. This is contrary to known facts regarding bacteria. Type species, *Spiroschaudinnia recurrentis.*

This genus is as yet not clearly differentiated from *Spirochæta* and may ultimately prove to be synonymous with it. The presence of an intracellular stage and the mode of infection through biting insects are the slender basis on which it rests at present.

In this genus Sambon has included two forms which produce relapsing fevers in man. One is *S. recurrentis* (Lebert 1874), better known by the synonym *Spirillum obermeieri* Cohn 1875, which is the cause of the relapsing fever common in Russia, the Balkan Peninsula, Turkey, Persia and India, and known by sporadic cases over the entire world. Patton has shown that the parasite is transmitted by the common bedbug (*Acanthia lectularia*) and possibly by the body louse (*Pediculus vestimenti*), although the evidence is not conclusive. The second species, *S. duttoni,* the cause of African relapsing fever, is difficult to distinguish morphologically from the foregoing, but is shown by experiment in animals to be distinct from it. According to Dutton and Todd the organism is transmitted by the tick, *Ornithodoros moubata*

(Murray). The young of infected ticks are capable of inoculating the disease and the spirochætes have been found in the eggs, where in fact they multiply and thus infect the new generation. This is evidently true hereditary transmission of disease.

A third species should be added to this genus, namely, the organism producing the relapsing fever of Bombay which Novy and Mackie have shown by inoculation experiments to be distinct from either of the preceding forms. To this form the name *Spiroschaudinnia carteri* has recently been given by Mackie. The disease caused by this species has been transmitted experimentally by a grooved needle and also by the bedbug, and none of the experimental animals contracted the disease in any other way than by inoculation.

In his outline Blanchard included one other genus, which with its diagnosis is as follows:

TREPONEMA Schaudinn 1905

Spiral body not flattened, but cylindrical in transsection, tapering towards the extremities. One flagellum at each extremity, no undulating membrane. Multiplication by longitudinal division, the initial stage of which may be identified by the doubling of the flagellum at one of the ends. Division forms remain long attached by their ends. Type species; *T. pallida.* One of the marked characteristics of this spirochete is the resistance to ordinary methods of staining. This stands in sharp contrast to conditions among bacteria. Gram's method and many others do not stain it at all, while no stain colors it deeply.

This form was discovered by Schaudinn and Hoffmann in syphilitic lesions; it has been experimentally transferred to apes, with the result of producing characteristic signs of the disease and has not been found in other diseases. Another species, *T. pertenuis* (Castellani 1905), which is regularly associated with the tropical disease known as framboesia, or yaws, also belongs here.

But even after these forms have been removed Blanchard's original list of the genus *Spirochæta* still shows an unnatural mixture of varied forms. Among the remaining species are undoubtedly those which form other natural groups and will later be assigned to new genera; but in the absence of fuller knowledge they may preferably be left for the present in the old genus. No doubt new forms will be added to this list. In this connection attention should be called to yellow fever and the view often expressed that the yet unknown cause of this disease will also prove to be a spirochete. Similarly the Miana disease of Persia known to be transmitted by a bird tick, Argas persicus, and other tick diseases in tropical and subtropical countries are thought to be due to the inoculation of closely related organisms.

Only two weeks later than the publication by Blanchard appeared an extensive paper by Novy and Knapp (1906). These authors recorded studies on a spirochete from a case of relapsing fever which was observed in Bellevue Hospital, New York. They regarded this form as identical with *S. recurrentis* and as the result of most careful studies reached the conclusion that the organism in question was undoubtedly a bacterium and not a protozoon. Their figures show strong evidence of transverse division and fail to indicate any trace of bodies which might be interpreted as nucleus, blepharoplast, or undulating membrane. They indicate also the presence of a single flagellum at one end of the spiral about as long as the spiral itself and with wavy turns corresponding in general to those of the spirochete, while a short process occurs at the other end. The staining qualities of the flagellum, the action of the organism under the influence of plasmolytic changes, its behavior both during and after being killed by heat and also the persistence of the spiral form under the most varied injurious conditions, are incompatible, in their opinion, with a protozoan nature and indicate affinity to the bacteria. The readiness with which these authors established active immunity is of-

fered as additional proof of the bacterial nature of the form with which they experimented, and finally they record the absence of a tendency to form layers around each air bubble, which is a very characteristic reaction for trypanosomes. Novy and Knapp conclude thus:

"The several facts which have been brought out under the preceding headings point clearly to the non protozoal nature of *S. obermeieri.* We must conclude, therefore, that the *S. obermeieri* belongs to the bacteria and more especially to the Spirillaceæ. As pointed out, the same conclusion has been reached by Borrel as regards *S. gallinarum* and *S. duttoni.* Three typical spirochetes are therefore demonstrated to belong to the group of bacteria.

"Hitherto it has been assumed that insect transmission indicates a protozoal organism, and in so far as the spirochetes are concerned, the chief evidence which can now be adduced in support of their animal nature is the fact of such transmission in the case of *S. duttoni* and *S. gallinarum.* The facts brought out in this study point so conclusively to the bacterial nature of the organisms that there can be little or no doubt of the correctness of the conclusion arrived at. With the recognition of this proof it follows that insect transmission is no longer a criterion of the nature of an organism."

Radical as is this critique of the animal theory of spirochete relationship, it has not been accepted as deciding the question, and has only provoked further discussion of the problem. Referring first to the question of insect transmission, it may be said that Koch has shown that the spirochetes multiply in the eggs of ticks and Carter that they undergo there changes as yet unexplained which may substantiate the claim of another cycle. Several investigators have found that in experimental animals they pass through the placenta from the maternal circulation to the fetal, although they undergo no changes consequent to this transfer. These observations do not accord with known facts concerning other bacteria.

Almost at the same time there was published an exceedingly careful investigation into the structure and development of the fowl spirochetes by Prowazek, with an appendix on a species from *Anodon* by Keysselitz, in which both authors come to conclusions diametrically op-

posed to those of Novy and Knapp with regard to the structure and relations of the spirochetes. It should be remembered that the species (*S. gallinarum*) on which Prowazek worked was one of those which Novy regarded as most positively of plant affinities. On the basis of most critical observations Prowazek indicates the presence of an undulating membrane with a conspicuous marginal cord. The body of this spirochete he finds to be flexible, a feature emphasized by various authors in the diagnosis of the genus. An analysis of the various types of movement shows, in his opinion, marked similarity to organisms possessing an undulating membrane or to the similarly provided sperm cells. Distinct granules lie in the axis of the organism which do not constitute a definite nucleus in the general sense of the term, but form chromidia such as are well known to occur frequently in the protozoon cell in the place of a single circumscribed nucleus.

So far as the conduct of these spirochetes towards reagents is concerned, the use of salt solutions did not produce the plasmolysis characteristic for bacteria even though the solutions were stronger than those sometimes successful in effecting this among the bacteria. Dilute alkaline solutions affected the spirochetes whereas the bacteria are very resistant towards them.

The identification and interpretation of the method of division is believed to be of especial importance in determining the systematic position of the spirochetes. In the opinion of Prowazek transverse division may occur, yet positive evidence demonstrated the occurrence of longitudinal division. Similar conditions in part were found on the species from the mouth (*S. dentium*), and were especially clearly illustrated by the observations of Keysselitz on a spirochete obtained from the fresh water mussel. Here the character of the undulating membrane and of the chromidia, the conduct of the chromatin granules in advance of division and the essential features of that process which was clearly longitudinal could be

most distinctly observed and delineated. Finally Prowazek calls attention to various protoplasmic accumulations or globules which make their appearance at certain times and in his opinion are not mere products of regeneration, but represent special resting stages in which protoplasm and chromatin granules experience involution. These peculiar processes have also been observed by other investigators on other species and may possibly be interpreted as particularly related to the sexual cycle.

Prowazek concludes that as regards the systematic position of the chicken spirochete (*S. gallinarum*), one is compelled on the basis of the structure, relation to reagents, manner of plasmolysis, and also on the basis of temporary cell parasitism to place the species among the protozoa and in close proximity to the trypanosomes. The undulating membrane was observed by Schaudinn in *S. dentium, refringens* and *ziemanni*. The existence of this structure can no longer be questioned. The large form discovered by Keysselitz suggests the large *S. plicatilis* and forms the transition to *S. balbianii* of the oyster which is without doubt closely related to the trypanosomes.

In a very recent paper Fantham (1908) demonstrates the occurrence and character of the spiral membrane in *S. balbianii* and *S. anodontæ*. He also explains the character of the movement as due to myonemes in the spiral membrane. Longitudinal division he finds to be frequent and to involve first the basal granules, then the membrane, next the chromatin masses and finally the body, the halves of which subsequently remain attached end to end. Fantham sees no clear evidence of sexual dimorphism, and finds the spirochætes non-plasmolyzable and without aerobic reactions. As characters manifesting bacterial affinities he lists the diffuse nucleus like spirilla; transverse fission even though infrequent, and the absence of a blepharoplast. Features suggesting protozoan affinities are the possession of a membrane, longitudinal fission, their non-plasmolyzable character

and several minor or doubtful factors. The spirochetes he believes to be distinct from trypanosomes in their less highly specialized structure, which exhibits morphological resemblance to bacteria.

In the face of such conflicting testimony on these morphological and physiological factors of primary importance for the interpretation of the group, one is compelled to seek collateral evidence to see if any can be secured which is definite, even though not in itself decisive. A few such indications are to be found among the uncontroverted records of various investigators. It is noteworthy that spirochetes resist culture in the media which serve readily for bacteria in general, and herein also resemble other protozoan saprozoites.[2]

Among indirect evidence one should note the work of Marchoux.[3] It has been observed that spirochetes easily lose their virulence. This author found that *S. gallinarum,* if passed through a series of birds, loses its lethal power and infectivity. In nature, however, the disease maintains its virulence, destroying entire broods in countries where it is endemic. The persistent virulence is thus seen to be related to the transmitting agent, the tick *Argas miniatus.* However, these ticks are incapable of increasing the virulence of a strain that has become attenuated and merely maintain any strain at its own level. These conditions do not resemble the action of bacteria, but, on the other hand, do simulate the conduct of protozoa, which pass through part of the life cycle in an intermediate host.

Another indication of much importance was furnished by Lingard in 1903 when he observed spirochetes in cattle penetrating red blood cells. Prowazek describes and figures in detail this occurrence in the fowl's blood where the parasite, after entering the corpuscle assumes a coiled or resting condition which he believes related in some manner to the (supposed) developmental cycle in the

[2] This convenient term introduced by Blanchard indicates at sight its meaning through analogy with the well-known botanical term, saprophyte.

[3] *C. R. Soc. Biol.,* 62, October 12, 1907.

intermediate host (*Argas*). Very recently Balfour (1907) has seen the spirochete actually enter the red corpuscle, and undergo changes within it in which the chromatin core is broken up into separate globules. This stage is very difficult to stain and has hitherto escaped emphasis. Some observers believe it to represent degeneration changes; even then it is incompatible with the theory of bacterial relationship, while, on the other hand, it suggests strongly conditions which prevail among other hematozoa. One is forced to note its great resemblance to the "latent body" of trypanosomes recently described by Moore and Breinl. This consists of a nucleated fragment of protoplasm which is stored up in spleen and bone marrow of infected animals and ultimately reappears in the circulation when it gives rise to a new trypanosome.

Jaffé (1907) has studied a form (*S. culicis*) found in mosquito larvæ and gives a careful analysis of the motile phases which stand in sharp contrast with the stiff screw movements of spirilla. He emphasizes also the ribbon-shaped body, the great susceptibility to solution of KOH even though very dilute, the axial nuclear (?) thread, and the occurrence of both transverse and longitudinal division.

The last work by Dutton and Todd (1907) demonstrated for *S. duttoni* a ribbon-shaped body with a central deeply staining core and a lighter periplastic sheath which at one end at least is prolonged into a flagellum. The central core does not stain uniformly, but has unstained areas and is sometimes broken up into granules. While these organisms occur singly, chains of three or four are frequent. They usually multiply by transverse fission, but longitudinal division also occurs periodically. Many forms taken from spleen and bone marrow are tightly coiled and a few of these undergo remarkable changes there. In the tick involution changes were observed including fragmentation of the chromatin. This process takes place in the Malpighian tubules where ap-

parently, the bodies burst and the granules become free to form the starting point for a new generation.

The group is evidently a doubtful one even yet. The occurrence of chains and of transverse division strongly favors a bacterial interpretation, but on the whole the trend of recent investigation has been to indicate its protozoan affinities and away from the earlier view of bacterial relationship. The spirochetes are certainly distinct from the spirilla and whether they are ultimately placed among bacteria or protozoa, it seems clear that they will occupy a more isolated position than has previously been assigned them by the advocates of either view. On the other hand, the recent proposal of Fantham to create for them a new group, the Spirochætacea, midway between the protozoa and the bacteria, can not be regarded as a helpful move. Such proposals in other groups have been found on later study to be evidence of an insufficient knowledge of the forms under consideration. Further investigation into the life history will undoubtedly furnish the definite evidence for a decision of the question.

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THE FAUNAL AFFINITIES OF THE PRAIRIE REGION OF CENTRAL NORTH AMERICA

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Those who are acquainted with the literature of the field zoology of North America are familiar with the fact, that, from the time of the Pacific Railroad surveys, naturalists have noted that there are in North America several well-defined biological regions. These have been pointed out at various times by Allen, Cope, Merriam and others, and the fauna of each has been more or less investigated. Of late years there has been a tendency among biologists to discredit this kind of work, owing to the apparent tendency of some naturalists to consider the mapping of these regions as an end in itself, but it seems to me that this work, if done properly, has a very real value.

If it is true that the formation of species among vertebrates is orthogenetic, as Whitman (1907) holds for pigeons, and I have found to be true in the garter-snakes (Ruthven, 1908), and these species are associated with different sets of environmental conditions, as seems to be the case, for example, in the genera Leptinotarsa (Tower, 1906) and Thamnophis (Ruthven, 1908), it is manifestly of importance that these areas of characterization be determined. Certain it is that the areas of characterization will not be the same for all animals, for the reaction of any form to any set of environmental conditions depends fundamentally upon the constitution of the animal, and this is a variable. On the other hand, in the case of terrestrial vertebrates, there would seem to be enough similarity in their mode of life to render

Map showing the location of the plains, prairie, and eastern forest regions of North America. (From Transeau, after Sargent.)

them subject to the same general conditions; a fact that is borne out by faunal studies. For example, we have forms of birds, reptiles and mammals characteristic of the plains region, others characteristic of the south-

eastern deciduous forest region, and still others characteristic of the northeastern coniferous forest region, etc. For these reasons it seems to me that careful faunal studies must contribute very materially to our knowledge of the affinities and relationships of forms.

Among the biotic regions that have been recognized in North America, the prairie region is one of the most interesting. It consists in general of a narrow zone separating the eastern forest from the semi-arid plains, as shown on the accompanying map. In Iowa, Illinois, northern Missouri, and southern Minnesota and Wisconsin, it widens into a wedge that extends to the western boundary of Indiana. Pound and Clements (1900), Transeau (1905), Bray (1901) and Sargent (1884) have shown that both the environmental conditions and the flora of this region are characteristic, but so far as I know the vertebrate life has never, as a whole, received examination.

During the past summer, the writer conducted an expedition[1] for the University Museum, University of Michigan, to northwestern Iowa, for the purpose of investigating the fauna of that region. The collections obtained by this expedition furnished a very representative series of the vertebrates of the prairie region, and a careful study of the data seems to lead to three fundamental conclusions.

1. *The peculiar environmental conditions of the prairie region have an effect upon the vertebrate fauna.* This is shown by the fact that many groups become modified as they enter this region from the adjoining ones. Note the following examples:

(*a*) I have elsewhere shown that as the snake *Thamnophis radix* (B. & G.) enters the prairie region from the plains it becomes strikingly dwarfed.

(*b*) Again, many of the plains forms are replaced in the prairie region by nearly related forms whose principal range is to the eastward of the prairie, as shown by the following instances:

[1] Detailed reports will appear upon the results of this trip.

Plains	Prairie
Western yellow-thoat, *Geothlypis trichas occidentalis* Brewst.	Northern yellow-thoat *Geothlypsis trichas brachidactyla* (Swains.).
Pallid horned lark, *Otocoris alpestris leucolaema* (Coues).	Prairie horned lark, *Otocoris alpestris practicola* Hensh.
Western grasshopper sparrow, *Coturniculus savannarum bimaculatus* (Swains.).	Grasshopper sparrow, *Coturniculus savannarum passerinus* (Wils.).
Sennett nighthawk, *Chordeiles virginianus sennetti* (Coues).	Nighthawk, *Chordeiles virginianus* (Gmel.).
Pocket gopher, *Geomys lutescens* Merriam.	Pocket gopher, *Geomys bursarius* (Shaw).

(*c*) Furthermore many of the forms from the eastern forest region are here replaced by others whose principal range is to the westward of the prairie. The following examples may be noted:

Eastern Forest	Prairie
Garter-snake, *Thamnophis sirtalis* (L.).	Red-sided garter-snake, *Thamnophis sirtalis parietalis* (Say).[2]
Blue-tailed skink, *Eumeces fasciatus* (L.).	Northern blue-tailed skink, *Eumeces septentrionalis* (Baird).
Long-billed marsh wren, *Telmatodytes palustris* (Wils.).	Prairie marsh wren, *Telmatodytes palustris iliacus* Ridg.
Chickadee, *Parus atricapillus* Linn.	Long-tailed chickadee, *Parus atricapillus septentrionalis* (Harris).
Meadow lark, *Sturnella magna* (Linn.).	Western meadow lark, *Sturnella magna neglecta* (Aud.).
House wren, *Troglodytes aëdon* Viell.	Western house wren, *Troglodytes aëdon parkmani* (Aud.).

2. *Most of the forms which inhabit the prairie region either extend also into the eastern forest region or into the plains region, or rarely both, few*[3] *being confined to*

[2] It is uncertain just which one of the Hog-nosed Snakes (*Heterodon*) is to be considered characteristic of the prairie region. *H. platyrhinus* Latr. has been recorded from the prairie region, and even from the plains, but the museum expedition only found *H. nasicus* B. & G. in western Iowa (Clay and Palo Alto Counties). The question can only be settled by detailed collecting and by the careful determination of the specimens.

[3] The pocket gopher, *Geomys bursarius* (Shaw), and the prairie hen, *Tympanuchus americanus* (Reich.), are exceptions to this rule, both being principally confined to the prairie region.

the prairie region. This composite nature of the prairie fauna may be seen by comparing the two lists above.

3. *There is a great difference in the extent to which the forms of eastern North America push westward, or the plains forms push eastward, into the prairie region before becoming modified or checked.* Among the plains forms the Arkansas kingbird (*Tyrannus verticalis* Say) and the western hog-nosed snake (*Heterodon nasicus* B. & G.) only extend into the western part of Iowa, Palo Alto County, being apparently the most eastern authentic locality recorded,[4] but the yellow-headed blackbird, *Xanthocephalus xanthocephalus* (Bonap.), and red-sided garter-snake, *Thamnophis sirtalis parietalis* (Say), extend into Illinois. Again, the prairie hare (*Lepus campestris* Bach.) and others only enter the western part of Iowa, while the Franklin spermophile, *Citellus franklini* (Sabine), penetrates eastward as far as Illinois, and the thirteen-lined spermophile, *Citellus tridecemlineatus* (Mitch.), extends to southeastern Michigan.[5]

Among the eastern forest forms, the Michigan mouse, *Peromyscus michiganensis* (Aud. & Bach.), cotton-tail, *Sylvilagus floridanus mearnsi* Allen, green snake, *Liopeltis vernalis* (De Kay), bluebird, *Sialia sialis* (Linn.), Baltimore oriole, *Icterus galbula* (Linn.), orchard oriole, *Icterus spurius* (Linn.), bob-white, *Colinus virginianus* (Linn.), swamp sparrow, *Melospiza georgiana* (Latr.), and others extend westward at least as far as the western margin of the prairie, while the Butler garter-snake, *Thamnophis butleri* (Cope), garter-snake, *Thamnophis sirtalis* (L.), meadow lark, *Sturnella magna* (L.), long-billed marsh wren, *Telmatodytes palustris* (Wils.) and many other forms, only enter its eastern border.

[4] The University expedition found the Arkansas Kingbird in Palo Alto County, and *Heterodon nasicus* on the line between Clay and Palo Alto Counties.

[5] Mr. P. A. Traverner has recently presented to the University Museum a specimen of *Citellus tridecemlineatus* (Mitch.) from Port Huron, Michigan, and Mr. N. A. Wood, of the University Museum, has observed a specimen in Oscoda County.

These facts, it seems to me, point strongly to the conclusion, that, as far as terrestrial vertebrates are concerned, the intermediate character of the environmental conditions makes of the prairie region an extensive area of transition between the plains and eastern forest regions, but that the environmental conditions are not either intensive or extensive enough to mold the forms into a peculiar fauna.

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PHYSIOLOGY[1]

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In the introductory lecture of the present course we were told that ours is the golden age of mathematics. As week after week has passed by since then, we have been led from one golden age to another, convinced, for the time, that the present brilliant achievements of each science outshine those of all the others. A few days ago I found on my desk an entomological monograph, the opening sentence of which reads, "The present age is the age of insects." I shall not attempt to harmonize the declarations of my Columbia colleagues with that of my entomological friend. But I feel that I should be derelict in my devotion to my own subject if I did not state frankly at the outset of my lecture—what ought, however, to be a self-evident truth—that the present is preeminently the age of physiology. Nor, following again the example of my predecessors, need I be over-modest in my claims as to the place of physiology in the scientific hierarchy. For Fick speaks of it as "the highest and most fruitful generalization of the collective natural sciences," and Czermak calls it "the summit of all the sciences."

It need not be emphasized that no exact boundary line exists for any one of the biological sciences. The proper domain of each extends, at its borders, imperceptibly into the domains of all, and within the boundary zones it is difficult to say what belongs to one and what to another. With this in mind it is impossible sharply to delimit the science of physiology. Nevertheless its proper domain is

[1] A lecture delivered at Columbia University in the series on Science, Philosophy and Art.

easily surveyed. Physiology deals with the process of life, the living of living substance. It is a dynamic, not a static science. The form, structure and composition of living things do not properly come within its scope: they form the subject matter of morphological, static sciences. But the changes in form, structure and composition, which are manifestations of the life process, are proper subjects of physiological study. Its material exists wherever life exists. Whether it be the growth of a man or of a tree, the creeping of an amœba or the contraction of a muscle, the beating of a heart or the production of a disease by a bacterium, the mental activity of a brain or the response of an infusorian to light, the process of reproduction or of inheritance, the phenomena of nutrition or the behavior of an organism to changes in its environment—all of these and a thousand others are physiological phenomena and proper subjects of investigation in the physiological laboratory. It is true that many departments of learning, which essentially are branches of physiological science, have been so far specialized in the methods of their pursuit and their aims and augmented by non-physiological additions, as to entitle them to specific names. In such cases it often is not expedient for physiology to busy itself with the more remote results of the operations of its laws. The great biologist of the last century, Johannes Müller, was wont to say, "*Psychologus nemo nisi physiologus.*" But, although psychic phenomena are inextricably linked with neural processes, the right of psychology to be recognized as an entity, with the study of psychic phenomena as its prerogative, has been abundantly demonstrated by its achievements. So, too, the proceedings of human society are the resultants of the action in human beings of physiological principles. But the study of the resultants themselves falls within the special province of the sociologist. It is thus customary to recognize as largely independent sciences, such branches of knowledge as psychology, sociology, neurology, biological chemistry, exper-

imental zoology, hygiene, bacteriology, pathology and preventive medicine; but in all these there is a large element of pure physiology, and their adherents often deserve the name of physiologists. When I say that the present is preeminently the age of physiology I mean it seriously, since at no time has the physiological spirit, the spirit of examining vital phenomena by the aid of experimentation, so completely permeated and vitalized the biological sciences as now.

There exist many misconceptions regarding the subject matter and scope of physiology. In the popular mind physiology deals with the life processes of the human body. In reality human physiology is but one of its many interests. It has its anthropocentric aspect. Biocentric it is in reality. The popular conception of physiology as a science of the functions of gross anatomical organs expresses, too, but a small part of the truth. During the middle part of the last century a powerful school of investigators in Germany busied themselves largely with the functions of organs, and strongly impressed the science of their time and the popular mind. But one of the pronounced phases of physiological development in recent years has been a similar rich growth of the study of the life processes of the cell. Another popular misconception is that physiology deals only with the internal parts of organisms—a view that is confuted by the fact that there is now going on much investigation of the mutual relations of organisms and their environment, in other words, an expansion of what has been called external physiology, which might bear the newer title of ecology. But the wide-spread ignorance regarding the broad scope of physiology is in part explained by the fact that a large number of professed physiologists do busy themselves with, and most academic courses deal largely with, the vital phenomena of the internal parts of higher animals with the image of man ever in the background. The chief cause of this condition in turn is doubtless the rise of the science within

medical schools and its continued close association with them, as a result of which the attention of investigators and teachers has been necessarily focused largely upon internal problems. This aspect of the science is mirrored in the text books, and is the chief aspect that is presented to the youth in his early studies. Unfortunately the university student has only a limited opportunity to correct his early false impressions, for the university has not yet accorded to physiology its rightful heritage as a pure science. Its freedom in research can not be denied it, however, and popular misconceptions regarding its scope will disappear with its advance. The living of the living thing is the criterion by which the physiological phenomenon may be recognized.

The ways in which the vital process manifests itself seem at first sight numberless and incapable of mutual comparison. The contraction of a muscle, the secretion of a glandular product, the production of a sensation, the growth of an organism, the orientation of a motile body to rays of light, the passage of a nervous impulse, respiration, the circulation of blood, the transmission of a quality from parent to offspring, instinct, fatigue, a volitional act, the course of a germ disease, sleep, speech, laughter, thought, the digestion of food, the maintenance of bodily temperature, the hearing of sound, sight, the recognition by touch of a familiar object, memory, emotions, the inhibition of an existing action, hypnosis—at first thought these phenomena appear to be of quite different kinds, each *sui generis* and incapable of comparison with the others. Have they common factors? Is it possible to unify them?

Through the ages various attempts have been made to do this. The appearance of the first of these attempts was nearly coincident with the culmination of Grecian culture. From that auspicious time down to the great Roman physician Galen, then across the long stretch of thirteen centuries, bridged by Galenic tradition, but barren of physiological discovery, to the rebirth of scien-

tific, together with other, learning, and well into the seventeenth century, the doctrine of the *pneuma,* or spirits, reigned supreme. This doctrine was often expressed in vague, uncertain terms, and in the hands of the Stoic philosophers, the Pneumatic physicians, the scientific men of Alexandria, Galen and minor writers, it was variously portrayed. The *pneuma* was believed to be an extremely subtile material agent entering the body with the breath, and was spoken of as "very subtle air," "very lively and pure flame," "fluid," "of the nature of light," "vapor," "something analogous to the spirits of wine," and so on. Each vital action was a manifestation of its activity. In the heart dwelt the vital spirits; in the brain the animal spirits. They flowed and ebbed through the veins and arteries, they coursed along the nerves, they permeated the tissues, and they bubbled and effervesced. Through them the body felt and moved, was nourished and warmed, grew and reproduced. It was a genial, comforting belief, nothing was more plausible; in its light vital actions seemed simple enough; and so for two thousand years the spirits danced merrily along.

But there were hard-headed thinkers in the seventeenth century. We may even imagine that the skilful experimenter, Harvey, the discoverer of the circulation of the blood, had his doubts. It is true that Descartes made free use of the spirits in his clever portrayal of the working of the organic machine, but there were others, believers in the machine, who contended that its *Deus* was not the *pneuma.* The spirit of mechanism was in the air. With the beginning of a rational physics, stimulated largely by the discoveries of Galileo and Newton, and a rational chemistry, freed from alchemy, there arose those two curious groups of Utopian theorizers, the iatro-physicists and the iatro-chemists, led, respectively, by Borelli and Sylvius. The one looked at the actions of the living being through the spectacles of the physicist, the other through those of the chemist; to the one vital actions

were physical phenomena, to the other, chemical phenomena. Their gaze was in the right direction, and each believed that he saw a great light. But like the whole world of science of their time, they knew too little of the true physics and chemistry, and their interpretations of organic processes, while containing a considerable modicum of truth, teemed with unwarranted hypothesis. It was not strange, therefore, that the iatro-movement was short-lived. Its influence, however, was not without value, for as the knowledge of physiological fact increased through experiment, and the world became accustomed to mechanical notions, the authority of the spirits became weakened, and gradually, very gradually, they ceased to be a factor in physiological reasoning. In popular speech, however, they persist even to our own day; for, as our moods change, we are in good spirits or bad spirits, full of spirit or lacking in spirit, high-spirited or low-spirited—phrases which stand as witnesses of a once powerful, but now discarded, physiological doctrine.

As the spirits became deposed, scientific thinkers, dissatisfied with the mechanism of the time, still groped for something to take their place. There were spontaneous uprisings of such agencies as Van Helmont's *archeus,* Stahl's *anima,* Boerhaave's *principium nervosum* and Hoffmann's ether. None of these long survived, and soon after the middle of the eighteenth century they were definitely replaced and the wide-spread desire for a unifying principle was for the time set at rest by the hypothesis of vital force. All physiologists had now come to realize that many of the chemical and physical phenomena of inorganic nature were to be observed also in living bodies. But they knew that the chemical composition of the latter differed from that of the former, and for the manufacture of the vital substance and for many of its actions they could find no parallel outside of living bodies. Most of them succumbed to the compelling power of their ignorance and acquiesced in the assumption that a peculiar principle resides in living

things, a vital force (or energy, as we would call it to-day), differing in nature from the forces (or forms of energy) that exist in non-living things. Johannes Müller presented the vitalistic conception clearly as follows:

"Organic bodies consist of matters which present a peculiar combination of their component elements, a combination of three, four, or more to form one compound, which is observed only in organic bodies, and in them only during life. Organized bodies, moreover, are constituted of organs, . . . each . . . having a separate function; . . . and they not merely consist of these organs, but by virtue of an innate power, they form them within themselves. Life, therefore, is not simply the result of the harmony and reciprocal action of these parts; but is first manifested in a principle or imponderable matter, which is in action in the substance of the germ, enters into the composition of the matter of the germ, and imparts to organic combinations properties which cease at death."

By the same author life is characterized as "the manifestation of the organic or vital force." Again, "Organic bodies participate in the general properties of ponderable matter. The laws of mechanics, statics and hydraulics are also applicable to them." The application of these laws to them is, however, "limited," from the circumstance that the causes of motion most engaged in them are essentially vital in their nature." A few bold spirits, like Reil in Germany and Magendie in France, argued against such a conception, but they formed a small minority, and the physiology of the time became essentially vitalistic.

This state of affairs prevailed for barely a century. Soon after its beginning oxygen was discovered, and the modern chemistry was begun. A few decades more and the new physics was founded on the doctrine of the conservation of energy. These two discoveries with their momentous consequences were epoch-making for physiology. The events of the inorganic world were at last conceived by the human mind in a rational manner, and the application of such conceptions to vital processes was not delayed. The assumption of a specific vital force was seen to be unnecessary. Men began to talk of vital phenomena in terms of the new sciences, and physiology

began to be defined as the science of the physics and chemistry of living things. Such is the prevailing conception to-day.

Is the vital process more than physics and chemistry? Two facts stand out strongly in the physiology of the present day. One is the constant extension of physico-chemical principles into the explanations of hitherto mysterious functions; the other the seeming inadequacy of those principles to explain other functions. In their attitude toward this apparent inadequacy physiologists, while disavowing with almost entire unanimity their belief in the vital force of a century ago, may be said to be collected at present into two camps. By far the majority, while not denying the existence of puzzling problems, are yet possessed of an optimistic spirit and look forward with serenity to the unraveling of the mysteries of the organism, as the mysteries of the inorganic become more clear. They look at life, not as a distinct entity permeating and vitalizing a complex machine, but rather as the sum of the activities of that machine. In the opposite camp there are a few souls who, though they too have cast off the dross of the old conception, are rendered impatient and despondent by the occasional failure of present knowledge to explain, and they fly for refuge to a refined and essentially inexplicable vital residuum. They have succumbed to the inevitable reaction that follows rapid progress. But they are not vitalists, they say, at least not paleo-vitalists: they are neo-vitalists. Into the intricacies of neo-vitalistic views and into the shades of difference existing between them it is not opportune here to go, for they exert practically no influence on the physiology of the time. The hopeful investigator continues his endeavors, and with success, to interpret vital processes in accordance with physico-chemical laws. It seems to me that this is the most promising method. For less than one hundred years has it avowedly been in vogue, and these have been the years of most rapid advance. In this time many mysteries seemingly inex-

plicable have been clarified. It is futile to deny future rapid progress along the same lines, and the solving of problems that now defy the ingenuity of the experimenter. We confess our ignorance and our frequent failures, but we believe that we are on the right track. Physics and chemistry are not completed sciences. Their youth indeed is hardly passed. Their greatest achievements are probably yet to come. If what we know of physical mechanism to-day is not sufficient to insure us an understanding of the physiological machine, then let us look to what we shall learn to-morrow. Whatever the ultimate outcome, the solace of the vitalistic conception, it seems to me, should be resisted until we are prepared with full knowledge to maintain the final inefficacy of the physico-chemical mode of interpretation. If such a time ever arrives, it must necessarily be far in the future.

If the vital process be capable of a physico-chemical interpretation, it is at once understood that the methods of the physiologist must be the methods of physics and chemistry. And this is the case. In the physiological laboratory we employ the same methods that are used in the physical and the chemical laboratories, modified only in so far as is necessary to adapt them to the material employed for study and the specific problems to be solved. Specific physiological apparatus of precision in great variety has been devised, and specific methods of using it. But the apparatus and methods are physical and chemical in essence. The physiologist's material for study must necessarily be living material, except in so far as it is possible to deduce the vital phenomenon from the phenomena of non-vital substances—a procedure which, though often necessary, as is especially the case in much of the work of the chemical physiologist, is a procedure of limited value. In external and in much of internal physiology the living organism is used intact. With many problems of internal physiology, however, the method of vivisection must be employed—a method, which, notwithstanding the occasional charges of the un-

informed, does not in either its theory or its practise imply cruelty or inhumanity.

Physiology has long since passed the stage where unaided observation alone is of value, and has become preeminently an experimental science. It is the task of the experimenter to alter one or more of the conditions under which the phenomenon occurs, to observe its change, if such appears, and thus to throw light upon the nature of the phenomenon itself, its relation to both its original and its changed conditions, and its causes. Herein lies the enormous difficulty of physiological work. The vital process is of a complexity unapproached, much less equaled, in the inorganic world. Living substance is never exactly the same at two successive periods. It is ever in unstable equilibrium, the seat of constant change, of augmentations and depressions, of physical and chemical mutations, and of what we in our ignorance call spontaneous activities; and the conditions of its activities are manifold and often obscure and unsuspected. To maintain the majority of these conditions intact, while altering one or more, is a superhuman task, one that is approached, but probably never realized in its entirety. The physiologist is thus constantly baffled in his pursuit of the desired object, and must needs exercise unwonted patience in the face of not infrequent failure. His progress is slow and his results can only approximate the mathematical exactness of the experimenter who deals with stable non-living matter.

Since the time when physiology assumed its physicochemical aspect and entered upon its modern phase, what has been the trend of its research? Its energies were first directed chiefly to the study of the mechanical and other physical problems of the organs of vertebrate animals. The electrical method of stimulating living substance was devised, by which the latter can be made to act at the will of the experimenter—a method the importance of which can scarcely be overestimated. The graphic method was early introduced and has been de-

veloped to the greatest refinement. By its use organic movements can be recorded graphically, and can then be easily analyzed into their space and time components and be studied at leisure. The working of the organs of the mammalian body, considered as physical machines, is now fairly well understood, although specific problems within this field are still being actively investigated. Very exact computations have been made of the amount of energy given off by the body in the form of heat and of muscular work, and it has been found to correspond very closely with the income of energy derived from the food and whatever bodily material may be consumed during the experiment. The principle of the conservation of energy applies as well to the living as to the non-living machine.

Chemical physiology, or, as it is now often called, biochemistry, developed gradually during the last century but did not become prominent until the last decade. It occupies now a foremost place among the branches of biological science. Much biochemical work is morphological; the determination of the chemical constituents and structure of substance once living, from which inferences may be drawn as to the chemical nature of living substance. Unfortunately, living substance can not be chemically analyzed directly, since all known methods at once kill it, and there is left only the non-living proteins, carbohydrates, fats and other organic and inorganic compounds, the individual bricks, or, better, cleavage products of the complex unity. In determining these and their relationships great progress has been made, but we of the present are far removed from that state of smug satisfaction of some of the earlier investigators, to whom a living body represented only so many molecules of carbon, oxygen, nitrogen, hydrogen, sulphur and phosphorus. The problems of the chemical physiologist, as distinguished from the chemical morphologist, are in general the problems of metabolism,—which the Germans have aptly styled "*Stoffwechsel*"—the chemical changes

undergone by matter in the process of living, its building up and its breaking down, its anabolism and its katabolism. The intricacies of metabolism can scarcely be conceived by one not familiar with the attempts to follow them, and the biochemists deserve much credit for the ingenuity of their methods. They have been most successful in determining and isolating the multitudinous katabolic products of vital activity, both the intermediate and the final products, and in discovering clues to the individual steps in the katabolic process. They have even succeeded in making synthetically many of these vital products, an achievement which was inaugurated by Wöhler in 1828 in the manufacture of urea. The laboratory synthesis of vital products has become, indeed, almost a daily occurrence and has hence lost its former miraculous appearance. It is not, however, certain that the laboratory methods and the physiological methods employed in such synthesis are identical. The steps of the anabolic process are still obscure, and until they are better known we can hardly look forward with confident satisfaction to the artificial manufacture of living substance. Yet physiological alchemists do exist, and the successful making of "life" has been heralded more than once to a sensation-loving world. Such an achievement is for the present only an idle dream, serving to gently and pleasurably titillate the cerebral cells of the dreamers.

Of recent years physiological physics and physiological chemistry have come to meet on common ground within the realm of the new science of physical chemistry. It has come to be clearly recognized that living substance consists of organic colloidal, or jelly-like, material, permeated by inorganic matter. The colloidal matter seems to consist of enormous complex molecules and aggregates of molecules; the inorganic matter partly of small, simpler molecules, and partly of ions, which are atoms or groups of atoms charged electrically. As the life process goes on, the living substance being now in a state of

activity, now in a state of rest, there is a constant chemical and physical interplay between the two material constituents, and a constant interchange between them and the surrounding medium, in which the laws of osmosis play a prominent part. The careful investigation of the nature of these internal and external exchanges seems to be illuminating many time-honored physiological enigmas, such as absorption, secretion, excretion and other instances of the passage of substances through membranes, the electrical phenomena of tissues, the nature of the nerve impulse, the fertilization of the ovum, and the general nature of chemical changes within protoplasm—enigmas which have been constantly quoted in support of the vitalistic conception. But we should not be tempted by success along these lines to claim, as is sometimes done, that the life process is merely ionic or electrical or osmotic in nature. In investigating physiological problems by the aid of modern physical chemistry, we seem to be brought at times periously near the electron theory of matter, and we are tempted to hazard the guess that the establishment of that theory would place the physiologist under renewed obligations to the physicist.

The study of ferments, too, is assisting—strange, innumerable, intangible bodies of uncertain nature, which, present in minute, almost imperceptible, quantities, seem to facilitate vital chemical actions without entering directly into them. In the early years ferments were recognized as mediating the processes of digestion, and but few of them were known. Of late their number has been enormously increased, and a corresponding number of intracellular or extracellular chemical processes has been ascribed to their action. Each has its own specific chemical reaction to facilitate, and, in many cases at least, their action is reversible, *i. e.*, one and the same ferment can aid both the decomposition of a complex substance into its constituents and the synthesis of those constituents into the complex substance. The ferments that function in vital processes are products of living matter,

but recent research makes it increasingly clear that they act merely like catalytic agents of inorganic origin. The study of ferments has its dangerous aspect, for more than one investigator, with an eye single to their universality and efficacy, has in his cyclopean enthusiasm come to suspect that all the chemical processes of living organisms are mediated by them, and has even been led to make the narrow and unwarranted assertion that life itself is merely ferment action.

The discovery of protoplasm and the establishment of the cell theory have exercised a profound influence on the science of function. Until nearly the middle of the last century physiologists were in a sense groping in the dark, for the reason that although they were endeavoring to unravel the mystery of living substance, they had no conception of the real nature of that substance. When the times were ripe they were quick to recognize the value and significance of the new discoveries, and, indeed, played valuable parts in formulating and establishing the new doctrines. With the clear recognition of a definite substance as the physical basis of life, their energies were more definitely directed than before. One result of this has been the increasing and powerful growth, during the latter part of the last century and the early years of this, of general physiology. The rise of general physiology represents a movement away from the earlier study of the mechanics of organs, toward that of the vital phenomena of living substance itself, irrespective of its special position within the organism. General physiology is preeminently the physiology of to-day, whether its point of view and methods be physical or chemical.

The principle of organic evolution is in its essence a physiological principle. It represents a great physiological experiment which nature has been making since the beginning of living things, and is continuing to make. But the discovery of the facts and principles of organic evolution and the establishment of its theory have been

accomplished only in small part by professed physiologists. Not even has the evolution of function—a field of great possibilities—been explored, except in a few small and isolated spots. The necessity of properly controlled experimentation in settling the vexed problems of evolution is, however, at last being recognized, and the next few decades promise to witness great advances in the discovery of the ways in which nature has made her great experiment.

It is not strange that with its intricacies and peculiar difficulties the solving of the problems of nervous function has proceeded slowly. The facts that nervous function is a property of the nerves, and that the brain is the seat of the mind were probably first capable of scientific proof by the Alexandrians in the fourth century before Christ. The two great functions of sensation and motion were also recognized by the ancients, but that they were mediated by different nerves was first demonstrated by Sir Charles Bell, so late as 1811. The idea of the specific energy of nerves—a phrase which means specific activity—or the general principle that each nerve has specific functions with which it always responds, no matter how stimulated, was definitely proposed by Johannes Müller in 1826 for the nerves of special sense, and later was generalized for other nerves and other tissues. Since then great progress has been made in discovering by experiment the specific functions of individual nerves and in formulating therefrom theories of the general functions of nervous tissues. That different nervous activities are associated with different portions of the brain was early surmised, and before the middle of the past century such important nervous centers as those controlling respiration and the beat of the heart became located. Since then the nervous mechanism of a host of unconscious organic processes has been discovered. That the psychic portion of the brain does not function as a unit, but consists rather of a complex group of nervous organs, each with its specific functions—a fact

that is of great moment in elucidating the relations of brain and mind—has been known for only a little more than thirty-five years. For it was in 1871 that Fritsch and Hitzig, by stimulating specific small areas of the surface of the cerebrum and obtaining in response specific muscular movements, first demonstrated a specific cerebral localization of functions. Since then the task of mapping out the outer layer, or cortex, of the cerebrum of a few mammals and man into centers, joined by nerve fibers with specific organs of the body and employed for the control of separate groups of muscles and for the work of the special senses, has proceeded to a considerable degree. Thus, we are now able to point to a certain portion of one of the convolutions of the cerebrum and say that its nerve cells, or neurones, mediate the volitional act of contracting one's biceps muscle; we can say that the neurones in other localities mediate the separate acts involved in locomotion; in others, the changes of facial expression; and in still others, the enunciation of thoughts in the form of spoken words. We know with considerable exactness the positions of the separate centers for sight and hearing; less exactly those of the other special senses. Besides the sensory and motor centers, evidence points strongly toward the existence also of cortical regions which are elaborately joined to one another and to the sensory and motor regions by means of innumerable nerve fibers, and the function of which is to correlate, harmonize or associate the work of the sensory and motor centers. Such association centers thus help to mediate the more complex psychical phenomena, such as memory and the association of ideas. We can even formulate helpful hypotheses of the neural accompaniments of various psychoses. According to James's theory of the emotions, for example, the perception of the automobile about to run us down leads to the feeling of fear only through the mediation of various organic processes, such as a quickening of the heart beat, pallor and trembling. The accompanying series of

neural processes would consist in the activity, in turn, of visual sense organs, neurones conveying the visual impressions to the brain, cerebral neurones mediating the sensation and perception of the terrifying car, motor neurones controlling the peripheral muscular actions that are involved in the organic processes, neurones conveying to the brain the impressions of altered heart beat, constricted arteries and trembling muscles, and lastly cerebral neurones mediating the feeling of fear. Because of its difficulty, much of the work of geographical exploration within the central nervous system is at present necessarily inexact, and moreover there is still much *terra incognita.* And even though we have thus come to know the gross functions of specific parts of the higher mammalian and human brains, we still know all too little of the processes by which the different parts are coordinated and made to subserve the many complex needs of the organism. The recent work of Professor Sherrington on the integrative action of the nervous system is an admirable example of the kind of investigation that is needed in this field, and by its very excellence helps to emphasize the lack of our knowledge. The laboratories of physiological psychology, now numerous, are making many valuable contributions, especially to our knowledge of the mechanism of the special senses. But when I make a summary of what we now know of the physiology of the nervous system, I come to realize anew its paucity, compared with what we ought to know and shall know, I am confident, in the long future. Here, it seems to me, is a field sadly needing tillage, and one where, though tillage be extremely difficult, the yield is certain to be rich.

All investigation here will lead up, in a sense, to the solving of that problem of problems, which has been for ages the focus of discussion and speculation, the problem of consciousness—"at once the oldest problem of philosophy and one of the youngest problems of science." For centuries it has been thought about, talked about, written about, and with what result? The elaboration of

hypothesis after hypothesis, which smell of the lamp—fabrications of the philosopher's cell rather than of the physiologist's laboratory. Almost without exception they are elaborate exercises in dialectics, rather than real portrayals of the nature of that most striking of physiological phenomena. To the physiologist they are almost without exception arid and unsatisfying. "Words, words, words," replies Hamlet to the question of Polonius. At first thought, the theories of dualism and interaction seem best adapted to the obvious facts of human experience: the brain and mind are two distinct entities usually intimately associated, and each capable of inducing phenomena in the other. But deeper brooding, and especially a recognition of the mode of action of the non-psychic portions of the nervous system and the close dependence of psychic on cerebral phenomena, of "how at the mercy of bodily happenings our spirit is," make us seek a more genuinely physiological explanation.

The physiologist recognizes as the morphological basis of nervous actions the neurone or nerve cell, consisting of a compact cell body, from which radiate outward filaments, the nerve fibers. He finds in the nervous system of the higher animal or man millions of such neurones and many more millions of nerve fibers. These constitute seemingly a confused and inextricable mass, but by careful study he has been able to discover an exact and definite, though excessively intricate, nervous architecture. He finds that the bodies of neurones act as central stations, to which and from which flow the nervous impulses along the nerve fibers: the incoming impulses constituting the centripetal, or afferent, or sometimes sensory, impulses; the outgoing constituting the centrifugal, or efferent, or sometimes motor impulses. He recognizes as the physiological basis of nervous action, the reflex action, consisting of an afferent impulse, a central process, and an efferent impulse. He sees reflex acts combined in innumerable ways, and augmented and depressed by other reflex acts. He sees many of the most

complicated actions of the individual performed with the aid of this reflex mechanism and without the aid of consciousness. He recognizes that a large proportion, if not the majority, of the individual's actions are reflex and unconscious actions. Lastly, he finds in reflex mechanisms no mysterious principle, but an ensemble of the same physico-chemical phenomena, which in one form or another he finds in other than nervous tissues, and in which the principle of the conservation of energy holds good. Turning now to conscious actions, he sees how indispensable to them, at least in the higher animal species and man, is a certain part of the cerebrum, especially the outer layer or cortex; and how the degree of intellectual development varies with the extent and complexity of this material structure. He sees how injury or disease of this part, or anything interfering with its proper activity, changes the individual from a sentient being into a non-thinking reflex machine. He sees acts, once consciously performed, now relegated to the unconscious reflex sphere. He sees how consciousness disappears in sleep, and how its manifestations vary under the influence of drugs. The cerebral cortex is composed of numberless neurones and is connected by afferent and efferent paths with the other portions of the nervous system. With these facts in mind, and though recognizing the intricacies of mental phenomena, the physiologist gets into the way of thinking that after all the mechanism of cortical actions is really the same as that of other nervous phenomena. He sees no objective, *a priori* reason why an entirely new causative principle should be introduced to explain the action of this small fraction of the nervous system. Whatever its nature, consciousness appears to him, not as a distinct entity grafted on to certain nerve structures, but as merely one of the modes of manifestation of the activity of those structures, just as chemical, thermal and electrical phenomena are other modes. Being thus one of the signs of nervous activity, the physiologist finds it difficult

to see how consciousness can act as a cause of nervous activity, any more than can the heat given off in such activity react to produce itself. The physiologist sees that nervous systems, with all their functions, have undergone an evolution; he recognizes orders of consciousness—a low, simple, gradual beginning, he knows not where, a progressive increase in complexity as nervous systems complicate, and the final culmination in self-conscious man. The relations of consciousness in its simplest form to the nervous system seem to be the same in kind as in the human being. For the physiologist, looking at the matter in this light, Huxley has probably formulated the best working hypothesis in his famous essay, "On the Hypothesis that Animals are Automata." After a lucid analysis of the actions of animals lower than man, he says:

"The consciousness of brutes would appear to be related to the mechanism of their body simply as a collateral product of its working, and to be as completely without any power of modifying that working as the steam whistle which accompanies the work of a locomotive engine is without influence upon its machinery. Their volition, if they have any, is an emotion indicative of physical changes, not a cause of such changes."

And later:

"It is quite true that, to the best of my judgment, the argumentation which applies to brutes holds equally good of men; and therefore that all states of consciousness in us, as in them, are immediately caused by molecular changes of the brain substance. It seems to me that in men, as in brutes, there is no proof that any state of consciousness is the cause of change in the motion of the matter of the organism. If these positions are well based, it follows that our mental conditions are simply the symbols in consciousness of the changes which take place automatically in the organism; and that, to take an extreme illustration, the feeling we call volition is not the cause of a voluntary act, but the symbol of that state of the brain which is the immediate cause of that act. We are conscious automata."

Objection after objection has been raised to the automaton hypothesis. It has been dialectically disproved many times. Its upholders have been charged with all the sins against logic, common sense, lucubration, spirituality and orthodoxy. And yet it will not down, for of all hypotheses it seems to accord most closely with the facts

of neural physiology, as we know them to-day. It may perhaps prove to be not a finality; but whether in the distant future it be found correct or incorrect, it is from its general standpoint, it seems to me, that the physiologist of the present epoch can do his most helpful experimental work. The problem of consciousness should be taken into the physiological laboratory, and the conditions of the manifestation of psychic phenomena should be investigated by laboratory methods. All mental processes, even to the last degree, are dependent on and have their basis in brain processes. The physiologist should study in minute detail the cerebral process of each mental act. He can thus inform the psychologist as to the conditions under which psychic phenomena occur. "An individual fact is said to be explained," says John Stuart Mill, "by pointing out its cause." And again, "The cause of a phenomenon is the assemblage of its conditions." In this sense the explanation of consciousness, it would appear, ought to come, sooner or later, from the physiologists.

I have spoken of the physiological aspect of other sciences. Pathology, the science of disease, or, in other words, perturbed function, is peculiarly close to physiology, for there is no sharp line of demarcation between the normal and the abnormal. We may assume the successive chemical substances involved in a certain progressive physiological act to be represented by the series *A*, *B*, *C*, *D*, in which *A* is the substance from which the chain proceeds. By analytic and synthetic processes *A* gives rise to *B*, *B* to *C* and *C* to *D*, which is the final end-product of the metabolism. Even with the same quantity of *A* and the same strength of stimulus, the quantities of *B*, *C* and *D* produced in successive repetitions of the act may vary considerably, owing to unknown factors. It is only when the intermediate or final products become markedly increased or diminished in quantity in comparison with their usual amounts, that we speak of the function as pathological. The excitability of cells may be greatly augmented or diminished and still be within the

limits of the normal. A tissue may grow excessively, as in tumors, or may waste away, and yet normal function be not seriously interfered with until remote limits are passed. Bacteria may live physiologically within an animal body. They produce and cast off toxins, which intrinsically are poisonous to the cells of their host. These, however, cause a physiological production of antitoxins in the body cells. So long as the antitoxins are sufficient in quantity and strength, they neutralize the poisonous toxins. If the latter get the upper hand they augment or depress the physiological activities of the cells of the host, and we speak of the result as a perturbation of function. The power of the organism to adapt itself to changed conditions and to maintain its physiological status is little short of marvelous. When, in spite of all endeavors, the physiological status is overwhelmed, then is the time for the pathologist to investigate and the physician or the surgeon to attempt to cure.

As in the biological sciences, so in the medical art, there exists a distinction between the morphologist and the physiologist, between the surgeon and the physician. The surgeon is the medical morphologist. His task is to remove diseased or injured tissue, to reunite separated structures, to restore structure or stimulate to its restoration, in short, to make structure normal, so that normal function may follow. The physician, on the other hand, is the medical physiologist. It is his endeavor to restore normal function. His life-long labor is an exercise in physiology. He should know his physiology as the surgeon should know his anatomy, minutely and to the last degree. He should know what health is before he tries to restore it. We all realize how rarely this ideal is reached, and we all have experienced the dire results of medical empiricism. Huxley likens nature and disease to two men fighting, the doctor to a blind man with a club who jumps into the mêlée, and strikes out right and left, sometimes hitting disease and sometimes hitting nature. Would not his blows be more telling if he were quite sure which of the combatants were nature and which

disease? Wherein he fails to avail himself of present knowledge he is culpable. And yet he is not to be charged with the whole burden of his failure to cure. Some of this should be shared, I regret to confess, by the physiologists, for they still know too little of the normal action of the vital mechanism. So far is this true, that I am convinced that one of the surest and quickest means of inaugurating a rational and effective art of medicine is through the advancement of physiological discovery. All physicians must be in part empirics until the physiological millennium is ushered in.

If I have been understood aright, my hearers will have perceived that with a mighty subject matter which is preeminently its own, physiology extends a leavening influence into a host of other sciences and medicine as well. It is an unusually good example of the typical pure science, with its outlying affiliations and applications. Like many another natural science, its rise, growth and early nurture were under the protecting wing of medicine. The physiologists of the early years, when their science was crystallizing out of the common mass of scientific knowledge, the men who first formulated its principles, and they who in later years developed it, were, with few exceptions, men of medical training who were under the influence of medical traditions and were guided by the medical spirit. In recent years the ties of the old traditions have been loosened, and the science is passing out from the parental shelter into the illimitable atmosphere of scientific freedom. Its aspirations in research are unhampered. Its achievements in research, in so far as it constitutes an academic theme, are limited by the fact that, except in a few isolated cases, physiology is still regarded by the university as primarily a medical science and its laboratories are housed in medical schools. This is a relic of early history. In consequence physiology must constantly breathe the medical atmosphere and must be influenced, whether it will or no, by medical ideals. This is not to be deprecated from the standpoint of physiological medicine, and the reciprocal advantage

to physiology itself in this one aspect is also great. But this now anomalous state of affairs leads directly to two consequences: namely, first, that the broader biological aspects of the science are less dwelt upon than otherwise would be possible; and secondly, that where such aspects have been investigated the work has been done largely by men not professed physiologists and usually lacking the latter's exact training as experimentalists. The customary academic position of the science thus imposes a certain restraint upon physiological progress, and delays its full fruition.

It is idle to try to predict the ultimate fate of the science that is attempting to make clear the vital process. To some minds it is attractive to speculate, and even to dogmatize, concerning the limits of natural knowledge. The present task of the physiologist is to investigate, and continue to investigate, ceaselessly and fearlessly, with a spirit ever fresh and hopeful, seeking only the elusive truth, unmindful of the limits of natural knowledge and undeterred by the fear that the mystery of life will ever remain a mystery. He must be content to spend his energies in patient laboratory research, accumulating facts, unifying facts and deducing laws for limited spheres of vital activity, and thus to lay the foundations for the broader generalizations that will come after his labor has ceased. By his constant association with the material substratum of the life process and the continual discovery of new and undreamed-of possibilities in its action, he gains a respect and even reverence for living matter which only he can possess. None but he can realize and understand its supreme beauty and harmony and sublimity. He can not sympathize with, much less share, the feeling that the material is base and only the spirit is uplifting, for to him the material makes its uplifting nobility manifest. He likes to believe, and to act on the belief, that no physiological problem is forever insoluble, and though ignorance may be long-lived, he sees no necessary reason for an ultimate, eternal *ignorabimus*.

NOTES AND LITERATURE

BIOMETRICS

Recent Contributions to Theory.—For obviously necessary reasons biometric work in the past has fallen, and for a considerable time in the future will continue to fall into two sharply separated categories. The first of these is the development of mathematico-statistical methods for dealing with biological material. The second is the concrete application of these methods to biological problems. Developments of higher mathematical theory will never be in and for themselves of particular interest to the great majority of biologists. Their only interest to the biologist exists in what they are practically good for; if there is developed any new mode of thinking or of investigation which will help to solve a problem it is of importance to know about it so that use may be made of it. The same consideration applies in regard to the applications of biometrical theory. To the biologist who is not cultivating this particular field of research the results obtained in it will be of interest only in so far as they appear to make significant contributions, expressible in terms intelligible to any non-mathematically trained person, to the solution of significant problems. There can be no doubt that valuable contributions to biology are being made by workers in biometry. Further, it is believed that this fact would be more generally recognized than is now the case, were the methods and results stated in a terminology less strange and repellent to the average biologist than is the mathematical. In accordance with this belief it will be the aim of these notes to set forth as clearly as may be and in a non-technical way the significant advances in biometrical research. Recent contributions to biometric theory will be considered in the present note. Work in the direction of the application of biometric methods to the solution of concrete biological problems will be discussed in subsequent notes.

The degree of trustworthiness of any reasoning from statistical constants of whatever sort must ultimately depend upon the values of the "probable errors" of these constants. The probable error is a measure of the limits of accuracy of the constant to which it applies. A number of recent papers deal

with various points regarding the general theory of probable errors. W. F. Sheppard, in a paper giving the mathematical proof of his corrections for the moments of frequency distributions,[1] points out that theoretically the raw value of the second moment rather than the value obtained by applying his corrections should always be used in calculating the probable errors of the mean and standard deviation. The present writer[2] shows by the consideration of concrete examples that the point made by Sheppard is not likely ever to be of any *practical* significance to the working biometrician. It makes no sensible difference in the actual result whether one does or does not use the corrected value of the second moment in determining these probable errors. In the same paper it is shown that a very considerable error may be made by using the formula ordinarily given for the probable error of the standard deviation when the distribution of variation differs considerably from the normal curve in certain particulars. One must always be cautious in assuming that a deviation from normality will be of no consequence in calculating probable errors.

A novel and important point regarding the probable error of a mean has been thoroughly investigated and solved by that mysterious person "Student,"[3] who has previously contributed to the pages of *Biometrika* under the same *nom de plume.* In passing it may be remarked that the propriety of publishing serious contributions to science under an assumed name seems questionable; one had supposed that those conditions no longer existed which in earlier times made such a course not merely desirable, but often indeed necessary if the same individual were to continue to contribute to science. To return to the point. In all kinds of experimental science the following type of problem very frequently arises; a series of say 10 or fewer experiments are tried under certain experimental conditions which may be denoted by the letters *a, b, c, d, . . . n*. A second series of equal extent is then tried with, say, one experimental condition changed so that the conditions are now *q, b, c, d, . . . n*. With what degree of probability may it be asserted that an observed differ-

[1] Sheppard, W. F. The Calculation of the Moments of a Frequency Distribution. *Biometrika,* Vol. V, pp. 450–459, 1907.

[2] Pearl, R. On Certain Points concerning the Probable Error of the Standard Deviation. *Ibid.,* Vol. VI, pp. 112–117, 1908.

[3] "Student." The Probable Error of a Mean. *Ibid.,* Vol. VI, pp. 1–25, 1908.

ence in the results of the parallel sets of experiments is *real*, that is, is due to the changing of condition a to q and not merely a chance result of random sampling? On account of the statistical smallness of such experimental series, coupled with the fact that the results usually deviate widely from the normal distribution of errors, the usual theory of the probable error of a class frequency or of a mean fails to give an adequate answer to the problem. "Student" has done the great service of providing formulas to cover the case. He furthermore gives a table of probabilities for series involving four to ten experiments, inclusive, wherefrom the answer to such a question as that propounded above may be read off at once when the experimental data are at hand. In the original paper concrete illustrations of the use of the table are given, based on published experimental data in the fields of physiology and of agriculture. No particular mathematical knowledge or skill is necessary to use this table and its importance to the experimental worker is obvious.

On this same topic of probable error Pearson and Lee[4] have recently made an important contribution. While the investigation itself is of a complex mathematical character, the essential point is this: Suppose a number of bodily characters (say six to eight) to be measured in a large sample of a population. There are likely to be a very few individuals out of the whole sample that differ rather widely from all the other individuals. What is the probability that such outlying individuals do not really (*i. e.*, biologically or genetically) belong to the population from which the sample is drawn, but only happen to get into the sample by accident? The solution to this problem is what Pearson and Lee attempt to give.

Along with these investigations on probable errors is to be included a recent paper of Pearson's[5] on the relation of past experience to future expectation. The nature of the problem discussed may be indicated by an example. Suppose that a sample of 100 individuals out of a population be examined and 2 per cent. of these individuals be found to be suffering from some particular disease. What percentage of a second sample of 100 may reasonably be expected to show the disease? The

[4] Pearson, K., and Lee, A. On the Generalized Probable Error in Multiple Normal Correlation. *Ibid.*, Vol. VI, pp. 59–68, 1908.

[5] Pearson, K. On the Influence of Past Experience on Future Expectation. *Phil. Mag.*, 1907, pp. 365–378.

answer usually given is that 2 per cent. is to be expected, with a probable error of a certain amount. In calculating this probable error in the ordinary way it is assumed that the distribution of chances is given by the normal or Gaussian curve of errors. Pearson shows that this is not true except (1) when the first sample is indefinitely large in proportion to the second, and (2) when the characteristic does not occur in either a very large or very small percentage of the population. He then proceeds to develop general formulæ from which one may determine first the average expectancy for the second sample and its true probable error, and second the frequency of future samples having varying degrees of the characteristic under consideration. These methods are fully illustrated with numerical examples. The usefulness of the methods for biological work may be indicated by an example. Suppose that in a sample of 200 tadpoles, 106 are males and 94 females. Suppose, further, that in a second sample of 300 collected later in the season the proportion is 171 males to 129 females. Is it to be concluded that between the collections some factor has come into operation tending to the greater production of males? Or, on the other hand, is the proportion exhibited in the second sample what might be regarded as a reasonable chance deviation due to random sampling in a population wherein the sex, determining factors had not changed since the first sample was collected? The paper under discussion furnishes the methods whereby questions of this sort may be definitely answered.

Another recent contribution of Pearson's[6] furnishes new methods of determining the degree of correlation between variates. The methods are adapted for use in cases where for one reason or another it is not feasible to use the ordinary product-moment method of finding a correlation coefficient. It is neither possible nor desirable to enter upon any detailed discussion of the mathematical features of these new methods here. Three new methods are given. The first, or "difference method" of determining correlation, furnishes a very simple and tolerably accurate way of deducing a correlation coefficient from a symmetrical (*e. g.*, homotypic) correlation table. The other two methods are con-

[6] Pearson, K. Mathematical Contributions to the Theory of Evolution —XVI. On Further Methods of Determining Correlation.

Draper's Company Research Memoirs. Biometric Series, IV, pp. 39. 1907. (London: Dulau & Co.)

cerned with the problem of determining correlation from material arranged in ranks. The most obviously simple way of dealing with any mass of statistical material is to arrange the individuals in a long row in order of ascending magnitude of some character. It is not even necessary that the character be accurately measurable on a quantitative scale to make such a row. The second, and on the whole most important of Pearson's new methods, shows how to deduce true variate correlation from the correlation of ranks. The method is less accurate than the usual product moment method. The third method deals with the determination of variate correlation from the positive difference of ranks. Regarding these last two methods Pearson's general conclusion is "that variate correlations found by ranks may prove to be a useful *auxiliary* method of dealing with correlation, when it is needful to give a rough answer to a problem in a brief time, or when the material itself is incapable of being accurately measured."

In connection with this matter of the analysis of statistics by the method of ranks or grades it is of interest to note that Galton has recently published a table[7] of deviates of the normal curve which will be found useful in practical statistical work. In the text accompanying the table (which is calculated by W. F. Sheppard) the use of the method of grades in dealing with material not susceptible of exact numerical measurement is discussed.

Of value for practical biometrical computing work is an editorial note[8] in the current number of *Biometrika* giving an easily calculated and extremely exact formula for the Γ function. This function is frequently used in statistical work, particularly in curve fitting.

RAYMOND PEARL.

PROTOZOA

Some Amœba Studies.—The amœboid organisms include a vast number of minute bits of glairy protoplasm which live in widely different places sometimes free in ponds and pools, sometimes confined as parasites, to the narrow limits of a single tissue. To

[7] Galton, F. Grades and Deviates. *Biometrika*, Vol. V, pp. 440–406, 1907.

[8] On a Formula for Determining $\Gamma(x+1)$. *Ibid.*, Vol. VI, pp. 118–119, 1908.

group all of these living things under the one generic name of Amœba is to confess the weakness and artificiality of classification. Schaudinn[1] attempted to bring some order into the group by adopting Cassagrandi and Barbagallo's generic name Entamœba to cover the ordinary parasitic forms of the digestive tract. These differ from the common *Amœba proteus* quite as markedly as do other genera of rhizopods, and whether they differ generically among themselves is a matter to be decided only when the life histories are made out.

Notwithstanding the hundreds of observations that are annually made on these amœboid organisms, there has been very little consecutive work on the changes of the protoplasm from beginning to end of the life cycle. Indeed, biologists would have extreme difficulty in picking up the thread of such a life history at either end, for observations and descriptions of conjugation or fertilization are most contradictory and confusing. The confusion will probably straighten out as soon as it is recognized that the varied accounts undoubtedly refer to quite different species or even genera of organisms. Schaudinn's description (*op. cit.*) of the process of fertilization in *Entamœba coli* was peculiarly daring, for autogamy amongst the unicellular animals was then a rare phenomenon, known to occur for a certainty only in Actinosphærium. Some such unusual process might be anticipated, however, in view of the fact that despite the thousands of eyes that annually study the amœboid forms, none have witnessed an ordinary form of conjugation amongst them. Schaudinn's excellent work on *Entamœba coli*, safeguarded by long experience with different kinds of protozoa study, and controlled by parallel studies on free-living rhizopods of other types must not be lightly brushed aside as too bizarre for serious consideration, especially as it has been confirmed in every detail by Wenyon[2] upon *Entamœba* (*Amœba*) *muris*, an intestinal parasite of the mouse.

According to Schaudinn, the cell of *Entamœba coli*, when mature, throws out all foreign matter and waste matter of its own metabolism, becomes more compact, smaller and spherical, and secretes a thick slightly refractive gelatinous membrane. The nucleus then divides by a primitive type of

[1] F. Schaudinn. Untersuch. über d. Fortpflanzung d. Rhizopoden. Arb. a. d. Kais. Ges.-Amt., XIX, 3, 1903.

[2] C. M. Wenyon. Observations on the Protozoa in the Intestine of Mice. *A. f. Prot.*, Supp. 1, Festband R. Hertwig, 1907.

mitosis into two nuclei which are separated from one another by the entire diameter of the cell. The nuclei then fragment, forming chromidia, while the cell becomes incompletely divided into daughter cells. In some cases the entire nucleus of each half disappears in the mass of chromidia granules; in other cases there appears to be a secretion of the chromidial substance as in Arcella, but in all cases a portion of the nuclear material is thrown out of the nucleus to degenerate. From the chromidia granules a new and smaller nucleus is formed in each half of the cell. Each then divides by a primitive mitosis into two nuclei, one of which degenerates, the other divides a second time and again one of the resulting daughter nuclei degenerates. After this process, which Schaudinn interprets as the equivalent of reduction and polar body formation in metazoa, the final encystment takes place. The gelatinous membrane disappears and in its place a much more refractive cyst membrane is secreted. The contents of the cyst become closely united again and the two remaining nuclei are brought together. Then follows a third division by mitosis characterized by long connecting strands which lie parallel with one another in the center of the cell and so that the daughter nuclei lie side by side in pairs. These paired nuclei then fuse, an eighth part of one of the original nuclei uniting with an eighth part of the other. Each cyst thus contains two fertilized nuclei, each of which subsequently divides twice to form eight nuclei. In this condition the cyst passes into the intestine of a new host, where the protoplasm divides into eight spores each with one nucleus. Wenyon's account of *Entamœba muris* confirms Schaudinn's in all essential features.

While *Amœba proteus* is probably far removed, phylogenetically, from Entamœba, there is reason to believe that the processes of fertilization have something in common. Four years ago Calkins[3] found what he regarded as evidences of a sexual phase in the life history, and described the multiplication of primary nuclei and the fragmentation of these nuclei into chromidia. The chromidia were interpreted as the possible nuclei of future gametes, an interpretation in line with the processes and outcome of chromidia formation in Foraminifera, in Arcella, Centropyxis, Difflugia and other rhizopods. Subse-

[3] G. N. Calkins. Evidences of Sexual Cycle in the Life History of *Amœba proteus*. *A. f. Protist.*, V, 1904.

quent observers, overlooking the fact that the stages in question must be very rare, have taken the ground, for the most part, that the evidence presented was too fragmentary to justify the conclusions reached. Some, like Schubotz,[4] while admitting the chromidia, claim that the organism is not *Amœba proteus*, and that the chromidia are not evidence of a sexual cycle; others like Prandtl,[5] forgetting that the cells under discussion were in a period of unusual physiological activity, attempted to explain them as pathological specimens with degenerating nuclei; and still others considered the scattered chromidia as possible parasites. The latter point of view was maintained by Prandtl[6] in a publication subsequent to the one just mentioned and in which the history of an Amœba-infesting parasite was made out. In this paper he hazarded the guess that the so-called multinucleate stage of *Amœba proteus* was in reality an ordinary form of Amœba infected with some species of Allogromia. This idea was undoubtedly suggested by the superficial resemblance between Prandtl's infected amœbæ and the photographs of the multinucleate *Amœba proteus.* Added experience would unquestionably have altered this conclusion, but the untimely death of this brilliant young investigator put an end to a career of great promise.

It was probably such experience that prompted Doflein to refrain from suggesting the possibility of an infection of *Amœba proteus* with some species of Dangeard's Nucleophaga. Doflein[7] found that the giant nucleus of *Amœba vespertilio* is a degeneration nucleus due to the presence of an intra-nuclear parasite *Nucleophaga amœbæa,* discovered by Dangeard in 1895, and he calls attention very properly to the possibility that many of the supposed chromidia in Amœba and allied forms may be parasites or stages of parasites of like nature. A similar parasite in the macronucleus of *Paramecium caudatum* was described by Calkins[8] as an intra-nuclear parasite similar to the intra-nuclear

[4] H. Schubotz. Beiträge zur Kenntnis der *A. blattæ* und *A. proteus. A. f. Protist.,* VI, 1905.

[5] H. Prandtl. Die physiologische Degeneration der *Amœba proteus. A. f. Protist.,* VIII, 1907.

[6] H. Prandtl. Der Entwicklungskreis von Allogromia sp. *A. f. Protist.,* IX, 1907.

[7] F. Doflein. Studien zur Naturgeschichte der Protozoen. V. Amöbenstudien. *A. f. Protist.,* Supp. 1, Festband R. Hertwig, 1907.

[8] G. N. Calkins. The Life History of *Cytoryctes variolæ* Guar. In Councilman's Studies on Variola. *Jour. Med. Research,* 1904.

phase of the smallpox organism. But between this parasite and the chromidia of *Amœba proteus* there is not the slightest trace of resemblance.

In the earlier paper it was supposed that the chromidia stage is only the antecedent of the later gamete formation and that conjugation of gametes is the method of fertilization. In a later paper Calkins[9] described some further studies made upon the same material after the amœbæ had been removed from the balsam, embedded in paraffine and sectioned. The supposed chromidia granules were then described as minute secondary nuclei which unite two by two, each couple giving rise to a reproductive body similar to a sporoblast. There were many gaps in this later account of fertilization and much remains to be done before the fertilization of *Amœba proteus* is established, but these later observations indicate a fundamental agreement with Schaudinn's description of fertilization in Entamœba. Chromidia formation seems to be an expression of some deeply lying biological activity concerned with the germ plasm and with fertilization. In some forms, as Arcella, Polystomella or Centropyxis, the nuclei of conjugating gametes are formed by the coalescence of such chromidia. In *Entamœba coli* there is a similar coalescence to form gametic nuclei, while fertilization is autogamous. In *Amœba proteus* the original nucleus of the cell divides repeatedly, the resulting nuclei break down into fragments, each of which is a complete gametic nucleus. Fertilization is again autogamous and chromidia formation s. str. absent.

It must not be forgotten in comparative studies of this kind that the organisms are widely different and that the expression of the fundamental biological activity underlying chromidia and fertilization is worked out in widely different ways. This obvious and trite observation has not been heeded in a recently published work on parasitic rhizopods by E. L. Walker.[10] Carried away, apparently, by success in raising amœboid organisms in large quantities by using artificial culture media recommended by Musgrave and Clegg, Walker has allowed to slip away a valuable opportunity to contribute something new to our knowledge of intestinal forms of rhizopods, while, on the other hand,

[9] G. N. Calkins. The Fertilization of *Amœba proteus*. *Biol. Bull.*, XIII, 1907.

[10] E. L. Walker. The parasitic Amœbæ of the Intestinal Tract of Man and other Animals. *Jour. Med. Research*, XVII, 1908.

he has allowed his imagination to lead him into generalizations involving totally different organisms. Here is one danger of the use of artificial culture methods in studying protozoa. The enormous numbers obtained tend to obscure the varying phases of vitality that characterize the life cycle of protozoa. The study of protozoa, even when it is possible to apply bacteriological methods, is fundamentally different from bacteria study. The latter dependent upon growth conditions, colony formation, reactions to media, etc., are essentially physiological. Protozoa study, on the other hand, is essentially morphological and is based upon the structures of the protozoan cell, involving all changes in cell structure which an individual (in the cyclical sense) undergoes during various phases of vitality. Hence it becomes necessary, first of all, to know the life history of a protozoon and the fundamental structures which its protoplasm assumes at different periods of vitality. Mere number of cells in any given phase is not satisfactory and here is where Walker falls into a trap. He fails to find stages described by Schaudinn and Wenyon, in his agar cultures and gives the inference at least that their observations were incorrect, all without taking the trouble to obtain his organisms in the corresponding stages of vitality. Schaudinn, in one set of observations to fill out the sexual phase of the life history, watched his material for weeks without finding the stages desired, and, to get them, finally swallowed the contents of a number of dishes, thus inoculating himself. His experiment was successful and he obtained what he wanted. This heroic method of procedure is not absolutely necessary, for abundant material may be obtained by inoculating lower animals; even such experiments, however, were not made apparently or, if made, not described by Walker. Such neglect vitiates all criticism or comment by the author, of conclusions of others regarding the sexual cycle of intestinal rhizopods and *a fortiori* of free-living *Amœba proteus,* an entirely different kind of organism.

Not even in regard to the ordinary vegetative phases of his organisms does Walker do justice to the material. The undoubted reproduction by budding is entirely overlooked; the term "spore" is misused throughout and the "extrusion" of fully formed reproductive bodies is very questionable. If such a method of endogenous bud-formation actually obtains, then, as an entirely new phenomenon in these rhizopods, it certainly

deserves more than the superficial description which the author gives. It is difficult to conceive how the budding process could have been overlooked, for in Entamœba under culture on agar, this process is apparently the most common method of reproduction. It is quite probable that development of the extruded so-called ''spores'' as described is the actual development of such buds. The finer details of structure were not made out, the origin of chromidia granules and their fate are not described, owing, possibly, as the author admits, to faulty technique (p. 418). Much dependence is placed upon the *cyst,* but there is no evidence to indicate that the author is cognizant of the difference between temporary and permanent cysts. Many instances among protozoa might be cited of the wide difference existing in the two types and in the same species, and Schaudinn and others have previously called attention to these differences in the parasitic rhizopods. Hence the cyst, as a feature in the identification of species as Walker gives them, loses it value. Walker's long list of species finally, while a convenient summary of the described amœboid parasites, can not be accepted as established, and his several ''new'' species must share the same fate, for in no case has the full life history—the only adequate basis of species—been made out. When the full history is worked out, these many so-called species will probably be reduced to mere varieties, or to a few species of the genus Entamœba.

G. N. C.

EXPERIMENTAL ZOOLOGY

Regeneration.[1]—Professor Korschelt has brought together in compact, yet readable form, the more important results on regeneration and transplantation in animals and plants. No small amount of discrimination is required to put into 170 pages all the results so far obtained on regeneration both of animals and of plants; yet Professor Korschelt has shown unusual judgment in selecting the essential and typical results of the old and the recent work. Necessarily, much detail has been pruned away, yet the author has succeeded in bringing into proper correlation many widely scattered facts. The more theoretical and analytical sides of the problem occupy a very

[1] Regeneration und Transplantation. By E. Korschelt. 1907.

secondary place in the present treatise, yet have by no means been entirely left out of account. We venture to think, however, that the more valuable outcome of the experimental study of regeneration lies less in a descriptive account of what takes place than in the attempt to give an analysis of the problems involved.

The second half of the book, some 75 pages, deals with Transplantation, or grafting, as it is more generally called. The more limited data in this field receive ample consideration.

The extensive literature of both subjects is arranged under topical headings—an arrangement that will recommend itself in the present case as preferable to the more usual methods of giving selected bibliographies at the end of each chapter or *en bloc* at the end of the book. We can not refrain, in passing, from calling attention to a slight misprint in one of the English titles that reads "The international factor in the regeneration of the tail of the tadpole."

Passing to a more detailed examination of Professor Korschelt's book, we find that while the formation of new growths in plants—more especially those cases where the new growth does not come from latent buds—is included under the heading of regenerative processes, the development of parts of the egg and the regulative changes that take place in isolated blastomeres and in fragments of the segmented egg are not included, despite the fact that the restoration of the whole form by a nucleated piece of a protozoon is described in some detail. Such limitations of the subject are, in the opinion of the reviewer, rather arbitrary; for, while it is unquestionably advantageous to limit certain fields, and to bring together certain groups of more closely related subjects, the fundamental problems of regeneration involved in all cases where a part produces a new whole have so much in common that the study of the subject gains rather than loses by taking as broad and as general an aspect of the subject as possible.

The most recent work on the regeneration of entire plants from leaves, as illustrated by the work of Goebel, Hildebrand, Winkler, Vöchting, Nemeč, Figdor and others is given in some detail in the opening chapter. It is pointed out that in many of these cases the new plant does not come from preformed buds, and not even from merismatic tissue in the case of Drosera according to Winkler, but directly from one or more cells of the epidermis of

the leaf. The problem of localization of the new growth in such cases is not discussed, nor have we, in fact, as yet any sufficient clue to the matter.

The growth of broken crystals in saturated solutions is dwelt on at some length. The remarkable similarity of this process to regeneration in organisms is emphasized, more especially in the light of the remarkable work of Lehman on fluid crystals. The author apparently suspends judgment concerning the interpretation of the resemblances of the two processes—whether we are dealing with only an analogous process or whether the two phenomena have fundamental properties in common. "Das Für und Wieder kann hier nicht erörtert werden."

Korschelt thinks that the loss of power to regenerate is a general accompaniment of the degree of organization (Organizationshöhe), yet he points out that this is not universal, as shown by the absence to regenerate in some forms and its presence in other closely related ones. In fact, the time-honored statement of such a relation has very little weight in the face of recent facts to the contrary. When, for example, such a complex organ as that of the eye of a salamander can regenerate from a piece of the bulb, while the head of the planarian, Dendrocoelum, fails to regenerate behind a certain level (where no obvious change in Organizationshöhe is apparent) we may well hesitate to lay any especial emphasis on such a generalization.

The discussion of the phenomenon of regeneration as an adaptation occupies only seven pages of the book. By adaptation is meant in general not so much that the process is useful—a fact too evident to dispute—but that *in some way* regeneration has been acquired on account of its usefulness. Our author would not, of course, adopt a teleological explanation, but assumes instead the supposed alternative of the Darwinian explanation of the origin of usefulness. Most students of the subject have rejected this interpretation on what the reviewer believes to be sufficient evidence. Korschelt's somewhat cautious attitude is summed up in the following statements. "Despite all the difficulties that have been raised one can not escape the impression that the power to regenerate and the liability to regenerate stand in a causal relation to each other." "We find that it is also the opinion of competent botanists that the interpretation of regeneration as an adaptation is little to the point. They agree with the zoologists mentioned above in this regard."

"If we look upon the power to regenerate as a property immanent in the living substance, which seems not improbable, owing to its wide occurrence, we may still suppose that this property has within certain lines of evolution been strengthened by adaptation and selection."

The origin of the new material from the old, the process of transformation (morphallaxis), the curious phenomenon of compensatory regulation, the occurrence of polarity and the development of heteromorphic structures are adequately dealt with from an objective standpoint, although in our opinion all too briefly considering the importance of the theoretical problems involved. These parts of the book are followed by a discussion of the factors of regeneration. The nature of the subject and the uncertainties of the theoretical problems involved make it difficult to treat such theoretical questions briefly and definitely, yet one could have wished that so admirable a review and so judicious a treatment of the descriptive processes might have been followed up by a more illuminating or at least suggestive discussion of the fundamental problems of regeneration as the title of this section might lead one to expect.

Under the heading of transplantation the grafting processes in plants is first briefly described. The important and recent results of grafting in animals receive careful attention. The interesting experiments on hydra by Wetzel, Rand, Peebles and King are sympathetically considered, and the equally important work of Korschelt's pupils, Joest and Rabes, are clearly and forcibly dealt with. Born's classical experiments with tadpoles, that have led to so many far-reaching experiments in recent years, occupy, as is their due, an important place in this field. The later work of grafting in amphibians, especially that of Harrison and Spemann, is described; but the author, while referring briefly to the important experiments of Lewes, has failed, in our opinion, to give them their proper place.

The author considers in some detail the modern work of transplantation of small portions of the tissues and has brought together in readable form the results of the literature of the subject, that is widely scattered, often in journals little accessible to zoologists. Korschelt's review will prove a useful source of information in such matters.

We cordially recommend Professor Korschelt's book as one of the most recent, most judicious and fair presentations of the

subjects of regeneration and grafting. The yearly reviews of Barfurth in the *Ergebnisse für Anatomie und Entwickelungsgeschichte* will supply special students with the numerous details that the study of regeneration is bringing to light. The more analytical and philosophical discussion of the problems involved will be found in the recent reviews and writings of Driesch. The general reader and layman who is less concerned with these details or with "the higher criticism" can not do better than give Korschelt's book a careful reading.

M.

PARASITOLOGY

A Chinese Parasite.—Looss has recently demonstrated[1] that under the old name "*Opisthorchis sinensis*" two human parasites have been confused by all save Baelz, whose differentiation of the two species in 1883 has been generally disregarded. For these forms the new genus Clonorchis is created with *C. sinensis* (Cobbold, 1875) as type. This species is the *Distomum inocuum* of Baelz and is chiefly a Chinese parasite, though it occurs rarely also in Japan. The other species is the *Distomum endemicum* of Baelz, which now becomes *C. endemicus*; it is the form usually described in text-books, etc., as "*Opisthorchis sinensis.*" According to existing records it is very common in Japan and presumably so in Annam and Tonkin also. It seems to be confined to localities on the sea-shore. I would suggest that this appears to indicate infection through fish, as is the case with *Opisthorchis felineus* in the territory adjacent to the Baltic.

H. B. W.

[1] *Ann. Trop. Med. and Par.*, 1, 123.

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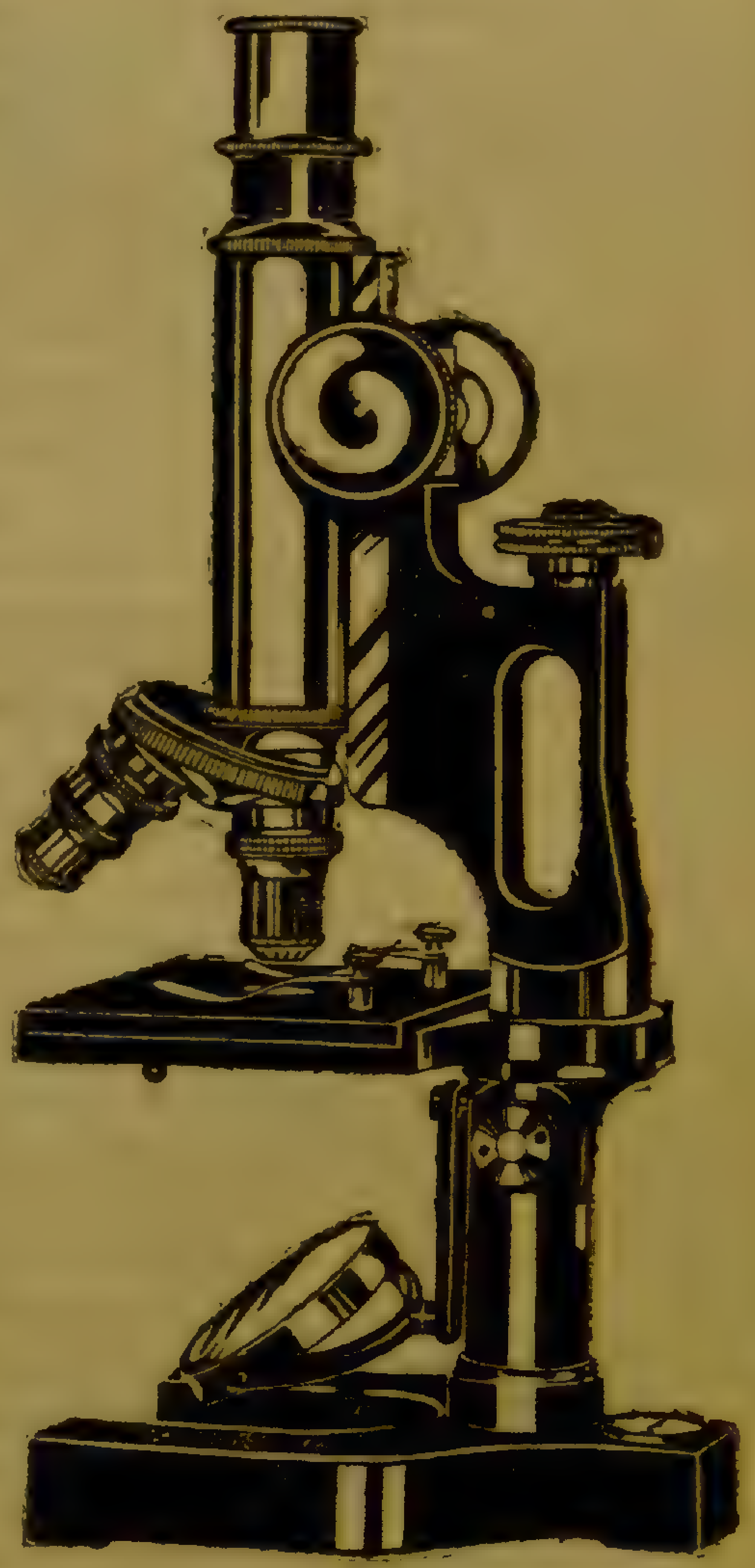

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Boston Society of Natural History,
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A NEW MENDELIAN RATIO AND SEVERAL TYPES OF LATENCY

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Introduction

In two papers presented before the Botanical Society of America at its annual meetings in New Orleans (1905) and New York (1906), I discussed the question of latency as exemplified by certain color-characters in common garden beans (*Phaseolus vulgaris*). These papers were published in reversed order in Science, May 7 and 24, 1907.

It was shown that certain characters appeared in the hybrids, of which no indication was found in either parent, and the origin of these novelties was traced to unseen Mendelian units possessed by the white bean (White Flageolet) used in the various crosses. The new characteristics were a mottled color-pattern, *M*, and a blackener or enzyme, *B*, which acts upon brown or yellow pigments, *P*, to produce anthocyan, the presence of the latter resulting in black or various shades of violet to reddish purple seed-coats. It was assumed that the brown and yellow beans used in these crosses have the gametic formula, *Pbm*, the black bean the formula, *PBm*, and the white the gametic formula, *pBM*. In crossing the white bean with any of the self-colored beans the three dominant units were brought together, resulting

in a purple mottled F_1 (*PBM*). It was the occurrence of this purple mottled F_1, no matter which pigmented bean was used, that led to my conclusions regarding the latency of a mottled color-pattern and a melanizer in the white bean, and also to the prediction that F_2 would consist of the five forms—purple mottled, black, brown mottled, brown (more properly, dark orange), and white, —in the well-known tri-polyhybrid ratio, 27 : 9 : 9 : 3 : 16.

AN UNEXPECTED RATIO AND ITS SIGNIFICANCE

At the time my last report was made, the count of the F_2 hybrids had not been completed, but the five predicted types were clearly presented. On summing up the results of the census of the numerous F_2 hybrid families, it was found that the ratio was not as predicted, but the mottled and self-colored beans occurred in all cases in approximately equal numbers, resulting in the ratio 18 : 18 : 6 : 6 : 16, or, reduced to its lowest terms, 9 : 9 : 3 : 3 : 8. To be exact, in the cross between Ne Plus Ultra (dark orange yellow, called "brown" in my notes) and White Flageolet, 10 families gave 133 purple mottled, 114 black, 40 brown mottled, 50 brown, 105 white, and 6 doubtful. Similarly, in the cross between Long Yellow Six Weeks (light yellow) and White Flageolet, 13 families gave 154 purple mottled, 159 black, 39 yellow mottled, 59 yellow (or brown), 160 white, and 12 unclassified. In the cross between Prolific Black Wax and White Flageolet, 3 families gave 53 purple mottled, 59 black, 44 white and 4 unclassified.

On comparing these results with those published by Tschermak[1] it is found that they are in perfect accordance with them, as he also found in a number of similar crosses, an equality between the mottled and self-colored beans. But our conclusions were diverse as to the source of the mottled pattern, I assuming that the mottled factor was brought into the combination by the white

[1] Tschermak, E. Weitere Kreuzungsstudien an Erbsen, Levkojen und Bohnen. *Zeitschr. Landw. Versuchsw.*, 7, pp. 533–638, 1904.

bean as a simple Mendelian unit, while he assumed that a mottled factor was carried as a "cryptomere" by the pigmented bean and that the white bean acts simply as a releasing agent or activator which allows or compels the latent mottling to become apparent.

The ratio 18:18:6:6:16 must have at first a very unfamiliar look to the student of genetics. It was not explained by Tschermak, but was separated by him into two groups of 9:3:4, wherein the interrelations of the several terms need no explanation.

The census of my second generation was completed shortly after the appearance of De Vries's[2] interesting account of "Twin hybrids" in Œnothera, and the suggestion lay at hand that this ratio presented by Phaseolus might be a case of twin di-hybrids, the first and second terms of the ratio, as also the third and fourth terms, being in each case different phases or aspects of a single unit, which might be expressed thus 9A:9∀ :3B:3ᗺ :8W. While such an hypothesis would fit the conditions presented by the F_2, it was seen very soon that it does not harmonize with the occurrence of a uniformly purple mottled F_1, nor with the splitting phenomena of F_3, a portion of which has been already examined. A consideration of the F_1 and F_3 shows that there are three distinct units involved, as was stated in my earlier papers, namely—a pigment factor, *P*, a blackener, *B*, and a mottled pattern, *M*.

If all of these characters behaved according to the simple Mendelian method, the ratio would be that previously predicted, and out of every 64 individuals, on an average, 27 would have purple mottled seeds, and 9 black. In order that the number of individuals having purple mottled seeds shall be equal to the number having black seeds, it is necessary that of the 27 that should on theoretical grounds be purple mottled, 9 must show no purple mottling but must be black, though it contains the dominant mottle factor, *M*. This group of 27 purple mottled

[2] De Vries, H. On Twin Hybrids. *Bot. Gaz.*, 44, pp. 401–407, D 1907.

individuals belonging to the theoretical F_2 ratio consists of the following eight types:

1 *PBMPBM*
2 *PBMPBm*
2 *PBMPbM*
2 *PBMpBM*
4 *PBMPbm*
4 *PBMpBm*
4 *PBMpbM*
8 *PBMpbm*
27

There is only one basis on which a group of 9 individuals having a common gametic feature may be derived from this group, namely, on the ground of homozygosis with respect to any single allelomorph. Thus, there are 9 homozygotes with respect to *P* (1 *PBMPBM* + 2 *PBMPBm* + 2 *PBMPbM* + 4 *PBMPbm*), 9 homozygotes with respect to *B* (1 *PBMPBM* + 2 *PBMPBm* + 2 *PBMpBM* + 4 *PBMpBm*), and 9 homozygotes with respect to *M* (1 *PBMPBM* + 2 *PBMPbM* + 2 *PBMpBM* + 4 *PBMpbM*), and the assumption that any one of these groups will give self-colored beans will answer the requirements of the empirical F_2 ratio, 18:18:6:6:16.

The only way in which it is possible to decide which of these three possible groups of 9 homozygotes is responsible for the equality of the mottled and self-colored types is to test their applicability to the other generations, since they all fit equally well the ratio found in the second generation. If homozygotes with respect to *P* hide the presence of *M*, it will be impossible to find an individual with mottled seeds which will not give a progeny, one fourth of which will be white-seeded; but of the F_3 families already examined, a number have been found which, while continuing to give mottled and self-colored beans in the ratio 1:1, have failed to produce any whites. If the homozygotes with respect to *B* are responsible for the latency of *M*, some brown or brown

mottled offspring would be produced by every purple-mottled parent, and there would be no equality between the purple-mottled and black in many families of the third and subsequent generations; but those F_3 families which have been thus far investigated show a number of instances in which purple mottled parents produce no brown or brown mottled young and there is a continued equality between the mottled and self-colored offspring of such parents. The remaining possibility, namely, that individuals which carry the mottled pattern, *M*, but are homozygous with respect to that character, are not mottled but self-colored, is the only one that fits all of the observed facts. The mottled color-pattern must be heterozygous in order to become apparent in the hybrids.

We may then indicate the composition of the group of individuals of F_2 which carry the dominant mottling factor, *M*, and the expectation as to the composition of the offspring which each will produce in F_3 as follows:

1 *PBMPBM* = Bl(Bl) (*M* latent in all).
2 *PBMPBm* = PM(1PM:1Bl) (*M* latent in ½ the Bl).
2 *PBMPbM* = Bl(3Bl:1Br) (*M* latent in all).
2 *PBMpBM* = Bl(3Bl:1W) (*M* latent in all).
4 *PBMPbm* = PM(3PM:3Bl:1BrM:1Br) (*M* latent in ½ the self-colored).
4 *PBMpBm* = PM(3PM:3Bl:2W) (*M* latent in ½ the Bl and ¾ the W).
4 *PBMpbM* = Bl(9Bl:3Br:4W) (*M* latent in all).
8 *PBMpbm* = PM(9PM:9Bl:3BrM:3Br:8W) (*M* latent in ½ the self-colored and ¾ the W).

It will be seen from this scheme that the mottled color-pattern could exist and does exist as a latent (*i. e.*, invisible) character in pigmented beans just as well as in the white bean, which is contrary to the assumption made, when I insisted that the mottled pattern must have come from the white bean. It is also obvious that the mottled

pattern could not exist in both the pigmented and white beans used in these crosses, as in that case the F_1 hybrids would have been homozygous with respect to this character and would have been black self-colored instead of purple mottled. In attempting to settle the question as to the origin of this mottled color-pattern I have carefully examined the results recorded by Tschermak and find evidence that at least one pure-bred pigmented bean must possess the mottled pattern while another does not. Whether the white beans used by him carried latent *M* can not be settled at present, but it is now plain that he may have been right in referring the mottling factor to the pigmented beans. My White Flageolet as well as all the white beans used by Tschermak may not have the mottled pattern, and the gametic formula of the White Flageolet should then be written *pBm*, instead of *pBM*.

This question can only be settled by further careful crossing. The evidence derived from Tschermak is as follows: In the cross between "Hundert für eine" (light yellowish brown) and "Mettes Schlachtschwert" (white) there was no mottling in the offspring; "Hundert für eine" crossed with "Schwarze Neger" (black), both self-colored, gave mottled offspring. Now according to my hypothesis, if "Schwarze Neger" carries the mottled pattern, "Hundert für eine" does not have it, and in turn, "Mettes Schlachtschwert" must not have it. If "Schwarze Neger," on the other hand, does not carry the mottled pattern, "Hundert für eine" has it, and in this case "Mettes Schlachtschwert" must also carry it. We can not say certainly, therefore, that the white "Mettes Schlachtschwert" does or does not have the mottled pattern, but on theoretical grounds either condition would be equally possible.

Among the corollaries of the explanation here given for the ratio 18:18:6:6:16 is not only the fact already given that the mottled pattern may be carried by the pigmented bean invisibly quite as well as by the white bean, but also, since the mottled beans are heterozygous with re-

spect to *M*, it would be impossible to have any of them breed true, *i. e.*, the mottled bean is in the same category in this respect as the famous Blue Andalusian fowl. This conclusion is supported by 48 families of the third and fourth generations reported by Tschermak and by over sixty families of the F_3 from my own mottled hybrids which have been already examined. Not one instance has been found in which the offspring of a mottled hybrid were even approximately all mottled.

The existence of pure-bred mottled races raises the interesting question as to what relation exists between these mottled hybrids which are heterozygous and can not breed true and the true-breeding mottled varieties. Tschermak[3] shows that in crosses between constant mottled races and self-colored races, the mottled pattern acts as a typical Mendelian dominant, the hybrids splitting in F_2 and subsequent generations in the ratio, 3 mottled : 1 self-colored.

Latency due to Separation

With respect to the question of latency since the purple mottling may not be a latent character of the White Flageolet, the type of latency discussed in my previous papers was only certainly exemplified by the pigment-changer, *B*, carried by the white bean. This type of latency is discovered by the production of a novelty when two allelomorphs are brought together, one or each of which, when acting alone, produces no visible character. Thus the black or purple color of these hybrids is due to the combination of the yellow or brown pigment of the pigmented parent and the colorless pigment-changer borne by the white parent. It may be called *latency due to separation* since patency is brought about by recombination. In my first paper on latency,[4] issue

[3] *Loc. cit.*

[4] Shull, G. H. Some Latent Characters of a White Bean. *Science*, N. S., 25, pp. 828–832, May 24, 1907.

was taken with Lock[5] regarding his assumption that novelties which appeared in crosses between certain peas were due to inactive units which became active on crossing. Lock[6] has since reconsidered that case and independently come to the same conclusion that I reached, namely, that the spotted seed-coat was introduced by the white-coated pea in which it was invisible owing to its separation from the pigment-producing factor. This is not an uncommon type of latency and seems to be the only type included by writers who have treated the subject of latency from the Mendelian view-point. It gives rise to such modifications of the Mendelian ratios as 9:3:4, 9:7, 27:9:9:3:16, 27:9:28, etc., instead of the theoretical 9:3:3:1 and 27:9:9:9:3:3:3:1. Some of these modified ratios are of more common occurrence, and are more familiar, than the unmodified ones, perhaps owing to the fact that albinism has been so frequently involved in the Mendelian investigations. Characteristics which are rendered latent by separation in the course of Mendelian hybridization have been called "masked" characters by Punnett.[7] This is not a particularly apt term for latent characters of this type, and would be much more appropriately applied to cases of latency due to hypostasis discussed below.

Latency due to Combination

The existence of mottling as a latent characteristic in pigmented beans, due to the fact that it only becomes apparent when in the heterozygous condition, is obviously of an entirely different type. Instead of being a phenomenon of separation, it is due to the union in the same zygote, of two dominant allelomorphs, either of which alone will produce a manifest character, but

[5] Lock, R. H. Studies in Plant Breeding in the Tropics. *Ann. Roy. Bot. Gard. Peradeniya*, 2, pp. 299–356, 1904. See p. 241.

[6] Lock, R. H. On the Inheritance of Certain Invisible Characters in Peas. *Proc. Roy. Soc.*, B, 79, pp. 28–34, 1907.

[7] Punnett, R. C. Mendelism. 2d ed., pp. viii + 85, 1907, London: Macmillan & Co. See pp. 47–53.

which, when acting together, produce none. This may therefore be called *latency due to combination,* since patency is brought about by separating the two allelomorphs whose union effaces their characteristic manifestation. If the White Flageolet carries the mottling factor, *M,* as was at first supposed, the appearance of mottling as a novelty in the first generation hybrids was due not alone to that fact, but just as much to the fact that the pigmented bean does not carry the mottled factor; or if, on the other hand, it should prove true on further investigation that the white bean does not carry the mottled factor, the mottled F_1 is due to this very fact, quite as much as to the fact that the colored bean does possess it.

The conclusion, reached in my previous papers, that the primitive bean was probably purple mottled and that the purple mottled condition is therefore an atavistic one, seems to be left in some doubt, because of the existence of two types of mottling, one of which behaves as a typical Mendelian unit as shown by Tschermak, the other having the peculiar faculty of losing its external manifestation the instant it becomes homozygous. I have no doubt that in some form the mottling unit is a primitive one, but whether the ancestral bean possessing that unit was mottled or self-colored would depend entirely on which type of the mottling unit it carried. In order to breed true it is necessary that both eggs and sperms shall all carry the mottled factor, and if this mottled factor were of the latter type, the beans produced by the union of such sperms and eggs, being homozygous with respect to mottle, would be self-colored, while if the mottle was of the former type, the homozygous beans would be mottled. The conclusion as to the allelomorphic composition of the original bean is probably correct, but as to its external appearance, it may as well have been black as mottled.

The peculiar behavior of the purple mottled allelomorph in my hybrids and in most of Tschermak's, may have a

very important bearing upon the interpretation of what are known as mid-races, *i. e.,* races which regularly produce two forms in about equal proportions, for, as has been seen, the mottled beans of all the hybrid families which did not have a mottled bean as one of its original pure-bred ancestors, constitutes a mid-race. This fact was recognized by Tschermak (*loc. cit.,* p. 47), though he attributed it to an unexplained effect of cross-fertilization, and not to the characteristic behavior of a definite Mendelian allelomorph. Other mid-races may likewise represent instances of latency due to combination. Wherever there is a double series of characters occurring in about equal numbers in the progeny of a self-fertilized individual, this type of latency should be looked for.

Purple punctation and brown flecking, which occur as novelties in the seed-coats of hybrid peas, were found by Tschermak to behave in a manner quite analogous to the mottling in beans, the first generation showing dominance of the novelty and subsequent generations always splitting into the punctate and non-punctate or the flecked and unflecked, respectively, and these no doubt are also cases of latency due to combination. Lock[8] has shown, on the other hand, that when certain mottled and spotted peas are crossed with self-colored peas, the mottling and spotting act as typical Mendelian dominants capable of extraction as characteristics of pure-breeding races, which ought to be expected, since the homozygous parental strains possessed these characters. The apparent discrepancy between his results and those of Tschermak will be fully explained if we assume that there are two types of these color-pattern characters in peas, as there are in beans.

In all of these cases of latency due to combination, the two units involved are of the same kind, so that the latency occurs only in the homozygous individuals, thus resulting in a striking contrast between homozygotes and

[8] Lock, R. H. On the Inheritance of Certain Invisible Characters in Peas. *Proc. Roy. Soc.,* B, 79, pp. 28–34, 1907.

heterozygotes. There are many other cases in which the homozygote and heterozygote show marked and often unexpected differences, the case of the Blue Andalusian fowl being one of the best known of these, but the heterozygous type of the Blue Andalusian fowl or other similar forms is not a case of latency at all, since no hidden allelomorph is brought to light as a result of heterozygosis, but only an unexpected external manifestation.

Latency due to Hypostasis

A third type of latency has also appeared in these bean hybrids, as best exemplified by a cross between the Prolific Black Wax and the Ne Plus Ultra, and between Prolific Black Wax and Long Yellow Six Weeks. In both of these crosses, besides the black and orange or black and yellow which were expected in the ratio 3:1, there have appeared a considerable number of beans of a dark seal brown or a dark greenish brown color. It is certain that these dark brown beans owe their color to the latency of a dark brown factor in the black bean. It has not been an infrequent occurrence to find black beans, not quite perfectly matured or which have been more or less weathered, that show this brown color apparently underlying the black. In this case the appearance of the novelty is due to the presence of a characteristic which can not be seen (*i. e.*, which is latent), for the simple reason that the black pigment possessed by the same bean is so intense as to cover over and hide the brown pigment. The independence of the brown and black pigments allows them to be separated into different individuals upon crossing the black with some other color.

Letting *D* represent this dark brown factor, the gametic formula for the black bean is *BD*, and for the orange brown and yellow beans, *bd*. This assumption leads to another rather unfamiliar modification of the Mendelian ratio, since the F_2 should consist of black, brown and orange or yellow in the ratio 12:3:1. The actual ratios are in essential accord with this expectation though there

are rather wide discrepancies due to the fact that the categories were not as carefully distinguished at first as they should have been. Thus in the case of the cross of Prolific Black Wax (black) with Ne Plus Ultra (dark orange or "brown") many of the dark brown beans were recorded at first simply as "brown," and the ratio found, 174 black:47 seal-brown:26 "brown," shows clear evidence of the extent of error thus produced. A deficiency of black is also apparent and is no doubt due to the recording of some weathered blacks, as dark brown. In the cross between Prolific Black Wax and Long Yellow Six Weeks, the deficiency in the blacks and corresponding excess in the dark brown is even more striking, giving the ratio, 155 black:55 dark brown:9 yellow:5 unclassified, theory requiring 168 black:42 dark brown:14 yellow. This factor *D* is also found to be present in the White Flageolet, where, like the black factor, *B*, it is latent by separation.

The occurrence of dark brown as an invisible character in the black bean may be called a case of *latency due to hypostasis,* following the terminology suggested by Bateson.[9] The unexpected character is not inactive, but its characteristic manifestation is invisible because it is hidden or inhibited by some other quality, and can only become visible when the overlying or inhibiting quality is removed by some means.

This type of latency is no doubt very common, as it is involved in many cases of simple dominance, as that term is generally understood. If the "presence and absence" hypothesis has general validity (and there is a very great preponderance of evidence in favor of it), the term "dominance" should be limited to the relation of the presence of any characteristic to the absence of that same characteristic, and should not be used for the relation between two different positive allelomorphs by virtue of which one hides the presence of the other. Bateson

[9] Bateson, W. Facts Limiting the Theory of Heredity. *Science,* N. S., 26, pp. 649–660, November 15, 1907.

applies the terms "epistatic" and "hypostatic" to the relative capacity of one unit to hide or to be hidden by another, owing to what I call latency due to hypostasis. As a simple illustration, a cross between a pea with yellow cotyledons, *Y*, and one having green cotyledons, *G*, shows *Y* dominant over its absence, *y*, and not over *G*. This would become immediately obvious if we could cross the yellow pea with still another type, say with one having colorless cotyledons. The correct gametic formula for the yellow pea is not *Y* but *YG*, in which the green is latent owing to the fact that *Y* is epistatic to *G*. The gametic formula of the green pea is *yG*.

That this is a correct interpretation of the apparent dominancy of one positive allelomorph over another is shown by some of my bean crosses. Thus Ne Plus Ultra (dark orange yellow) crossed with Long Yellow Six Weeks (light yellow) produced in 14 F_2 families, 382 orange yellow:130 light yellow, an apparent dominance of orange over light yellow. That the light yellow is latent in Ne Plus Ultra and is not the recessive condition of the orange yellow allelomorph is proved by the fact that in the F_2 families of the cross between White Flageolet and Ne Plus Ultra, light yellow beans appear. Letting *O* represent the orange allelomorph and *Y* the yellow one, the gametic formula of Ne Plus Ultra with respect to these two factors is *OY*, that of the yellow bean is *oY*, and that of the white bean likewise *oY*.

The ratio, 12:3:1, presented by the crosses of Prolific Black Wax with Ne Plus Ultra and Long Yellow Six Weeks, has been reported for but one other case so far as I know, though it ought not to prove very uncommon. It will appear in the F_2 of any cross which produces an F_1 of the form *ABCab* with *B* hypostatic to *A*, *C* hypostatic to both *A* and *B*, and neither *A*, *B*, nor *C* latent from any other cause. In these beans the crosses are of the type $ABC \times abC = ABCab$, *i. e.*, both *B* and *C* are latent in the one parent and no latent characters are demonstrated in the other. The same ratio will result from a

cross of the type $AbC \times aBC = ABCab$ provided the same relations exist among the several allelomorphs as before. In this case the character C is latent by hypostasis in both parents. This condition has been realized by Toyama[10] in hybrids between the common Japanese white silk-worm and the Siamese striped silk-worm in both of which a "pale," unmarked type is latent by hypostasis. The F_1 is uniformly striped like the Siamese, and the F_2 consists of striped, "white," and "pale" in the ratio 12:3:1. Toyama's statement that the "pale" character was in the "dormant" state indicates a misconception of the nature of latency due to hypostasis.

Latency due to Fluctuation

Another very potent cause of latency is to be found in fluctuation. It is well known that many of the less marked qualities of plants do not appear under unfavorable conditions of growth. By growing the offspring of these poorly developed individuals under favorable conditions they may be shown to possess all the characters of other members of the race to which they belong. Invisibility produced by this cause may be called *latency due to fluctuation*. Patency is brought about by good feeding, room for full individual expression, etc. As a specific example, I may mention my experience with several biotypes of *Bursa bursa-pastoris* (L.) Britton. These differ from one another by certain characteristic lobings of the leaves, and these characters have proved, on crossing, to be typical Mendelian unit-characters. However, by growing the plants belonging to any of the several biotypes under sufficiently unfavorable conditions they may be made to produce seeds while bearing only the unlobed juvenile type of leaf. The Mendelian rosette characters are then wholly invisible or latent. If the

[10] Toyama, K. Studies on the Hybridology of Insects. I. On some silk-worm crosses with special reference to Mendel's Law of Heredity. *Bull. Coll. Agr. Tokyo Imp. Univ.*, 7, pp. 259–393, pls. VI–XI, July, 1906. See pp. 348–353 and pl. X, III, *a*, *b*, and *c*.

offspring of such plants are grown under favorable conditions the latent characters are again rendered patent, showing that the loss of external manifestation has had no influence upon the allelomorphs themselves; they were present in the badly developed specimens, but were invisible because a sufficiently late stage of differentiation was not attained to permit them to express themselves.

Another striking case in which the latency of a Mendelian character, perhaps due to fluctuation, has been fully demonstrated, is in the cross between blue and white Indian corn investigated by Lock.[11] The blue is, in general, dominant over the white, but the white grains are always in excess of expectation, sometimes more, sometimes less; subsequent breeding tests with the whites show that a sufficient proportion of them are heterozygous, instead of extracted recessives, to make up the deficiency found in the number of blues in the preceding generation. It is not impossible, as Lock suggests, that further investigation of this case will discover some other cause than fluctuation for the latency of the blue aleurone layer in these white-grained heterozygotes.

The classic case of so-called "double adaptation" in *Polygonum amphibium* which is pubescent in its terrestrial form and glabrous when grown as an aquatic, and other cases of the same kind, present illustrations of latency due to fluctuation, instead of being due to the presence of two antagonistic determinants whose activities are mutually exclusive as suggested by De Vries.[12]

The very common occurrence of latency due to fluctuation must have an important bearing upon the significance of cultural conditions for the production of variations. There has been much diversity of opinion on this point, the general impression being that cultivation and the removal of competition are very potent in inducing

[12] De Vries, H. Species and Varieties, their origin by mutation, pp. xviii + 847. 1905. Chicago: Open Court Pub. Co. See p. 430 *et seq.*

[11] Lock, R. H. Plant Breeding in the Tropics. III. Experiments with maize. *Ann. Roy. Bot. Gard. Peradeniya*, 3, pt. 2, pp. 95–184, November, 1906. See pp. 144–163.

variation, and that in consequence of this fact it is improper to apply principles derived under cultivation to plants growing free in nature. There can be no doubt that good cultural conditions render patent many internal characters which are invisible under conditions of poor nutrition and crowding, and this fact together with the fact that many of the common culture-plants are complex hybrids, may fully account for the general impression regarding the effects of culture. There is no satisfactory evidence that good feeding and other conditions usually supplied under tillage have any effect in the production of the mutations upon which the external characters no doubt ultimately depend.

General Considerations

It is obvious from the foregoing results and discussions that latency is not a simple phenomenon, but may be due to a number of different circumstances. The point which I have strongly emphasized in my two preceding papers on the subject of latency—namely, that cases of latency must be explained, not upon the ground of inactivity or dormancy of characteristics, but simply on their invisibility— is fully borne out by all the facts here presented. The several different types depend upon the different causes for the invisibility of the characteristics.

Of the four types of latency here recognized, the first three types—those in which latency is due to definite interrelations between Mendelian units—will give rise to definite characteristic ratios which are as constant for each case as the typical ratios are for typical Mendelian phenomena. This is not so with latency due to fluctuation, as the variable conditions upon which the fluctuations depend may be such that any proportion of the individuals from none to all may have the character in question latent. This is not only true of the characters of pure-bred types as exemplified by *Bursa bursa-pastoris*, but is even more apt to be true of heterozygotes, thus resulting in many deviations from the correct ratios, as

seen in Lock's blue × white corn cross and doubtless in very many other cases.

It is probable that many discrepancies between actual and theoretical ratios are due to some sort of latency. This will generally be detected readily in subsequent generations, and no one should be hasty in declaring that a character which is of the splitting kind is non-Mendelian until the various types of latency are considered which may have taken part in modifying the ratios. "Variable potency," "contamination" or "impurity" of the gametes, and "alternating dominance" will all need to be reconsidered and in some cases reinvestigated, before they can have any secure standing as exceptions, amendments or additions to the simple law of "purity of the gametes" which is the essence of Mendelism.

There is still another way in which unexpected ratios may be produced, without in any way affecting the fundamental principle of the purity of the gametes, their production in equal numbers, and their union according to the laws of chance, and while the question of latency is not involved in this case, it deserves to be mentioned in this connection. Baur[13] has shown that in a variegated race of Antirrhinum, the variegation belongs only to the heterozygote. The extracted recessives are green and the extracted dominants fail altogether to appear, owing evidently to the fact that the zygote so formed is incapable of development, the ratio resulting from self-fertilization of the heterozygotes being therefore 2:1. It is conceivable that every degree of inefficiency of zygotes formed by the union of two particular allelomorphs might occur and thus quite various modifications of the expected ratios be the result, when those ratios are determined by a count of the successful zygotes. This cause for the failure of the expected ratios is certainly of rare occurrence, but like questions of latency it can be demonstrated

[13] Baur, E. Untersuchungen über die Erblichkeitsverhältnisse einer nur in Bastardform lebensfähigen Sippe von *Antirrhinum majus*. *Ber. Deutsch. Bot. Gesell.*, 25, pp. 442–454, 1907.

without difficulty by breeding tests, and these should be made before any new principle is invoked, or the old and well-founded principles are declared invalid, in the attempt to account for such discrepancies.

SUMMARY

The foregoing discussion and conclusions may be summarized thus:

In certain bean hybrids, mottled seed-coats depend upon the presence of a mottling allelomorph in a heterozygous condition, the homozygous condition giving unmottled seeds. This peculiar situation results in a tri-polyhybrid ratio, 18:18:6:6:16, instead of the usual ratio, 27:9:9:3:16.

Latency is held to mean invisibility, and not inactivity or dormancy, and four types are recognized, according to the different causes of invisibility; still other types may be found. The four types discussed in this paper are:

(*a*) *Latency due to separation,* in which an allelomorph when acting alone has no external manifestation and is only rendered patent by combining it with another allelomorph. Such latency gives rise to the ratios 9:3:4, 9:7, 27:9:9:3:16 and 27:9:28, instead of the theoretical, 9:3:3:1 and 27:9:9:9:3:3:3:1.

(*b*) *Latency due to combination,* in which two dominant allelomorphs, each giving rise to a peculiar character when acting alone, lose their external manifestation when co-existing in the same zygote. Upon self-fertilization this type of latency gives rise to such ratios as 1:1, 3:3:2, 18:18:6:6:16, etc., and may be found to account for the existence of certain mid-races, and other cases in which a double series of characteristics are presented in nearly equal numbers.

(*c*) *Latency due to hypostasis,* in which the presence of one allelomorph can not be detected owing to the presence of another allelomorph, the character produced by the latter being unmodified by the activity of the former. This type of latency is exemplified by the black bean

which hides the presence of a wholly distinct brown allelomorph, and a dark orange bean which carries invisibly a light yellow allelomorph. This condition gives rise in one series of crosses to the ratio, 12:3:1. Properly the term "dominance" should be limited to the relation between any positive characteristic and its own absence. Whenever one positive character seems to dominate another positive character, the latter is latent by hypostasis in the individual possessing the former.

(*d*) *Latency due to fluctuation,* a very frequent phenomenon in which characteristics disappear under conditions of poor nutrition, etc. Cultivation under favorable conditions makes such characteristics patent and this fact may account in part for the general impression that cultivation induces variation. Cases of "double adaptation" are examples of this type of latency.

Many discrepancies between theoretical and empirical inheritance-ratios are due to latency, and care should be taken to investigate the possible latencies which may be present before declaring that a character is non-Mendelian, because of a discrepant ratio. "Variable potency," "contamination" or "impurity" of the gametes, and "alternating dominance" which have been proposed to account for the appearance of various novelties, or of deviations from expected ratios, can have no secure standing until the question of latency in the sense of invisibility has been taken into account.

A modification of expected ratios may rarely result also from the failure of certain allelomorphs to make vigorous zygotes when joined together in certain combinations.

THE LEG TENDONS OF INSECTS

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WHILE perhaps known to working morphologists, the fact that the leg tendons are cuticular invaginations, and therefore subject to replacement at each molt, does not appear to have attracted the attention of any of the writers of text-books, and as far as the writer of this article is aware, has not been published at all.

The three best developed tendons are the two operating the knee joint and the one that flexes the claws. These three are almost invariably present, though one or the other may be very short, or present only as a cuticular thickening.

These structures are very easy to study in small insects. I have found aphids the most satisfactory subjects. The legs of most species are transparent enough to show the structures well when mounted whole, and the exuviæ are especially satisfactory objects. They may also be obtained in such abundance that one can mount large series of specimens, thus obtaining mounts showing the legs from almost any desired point of view.

The knee joints provide for the largest amount of motion of any of the joints of the leg, and this motion is all maintained in one plane by the development of two bearing points, making a hinge. The end of the tibia is small enough to telescope within the femur but for these articular processes. They consist of a process projecting inwardly on either side of the rim of the femur, as shown in Fig. 1, *A* and *B*, and corresponding with these femoral processes there are slight outwardly projecting processes from the margin of the thickened rim of the tibia. The articular membrane at these points prevents the displacement of the processes.

The whole dorsal end of the tibia, including these processes, is very largely hardened and thickened and marked off from the body of the tibia by a deeply infolded ridge. Most of this thickened portion is within the end

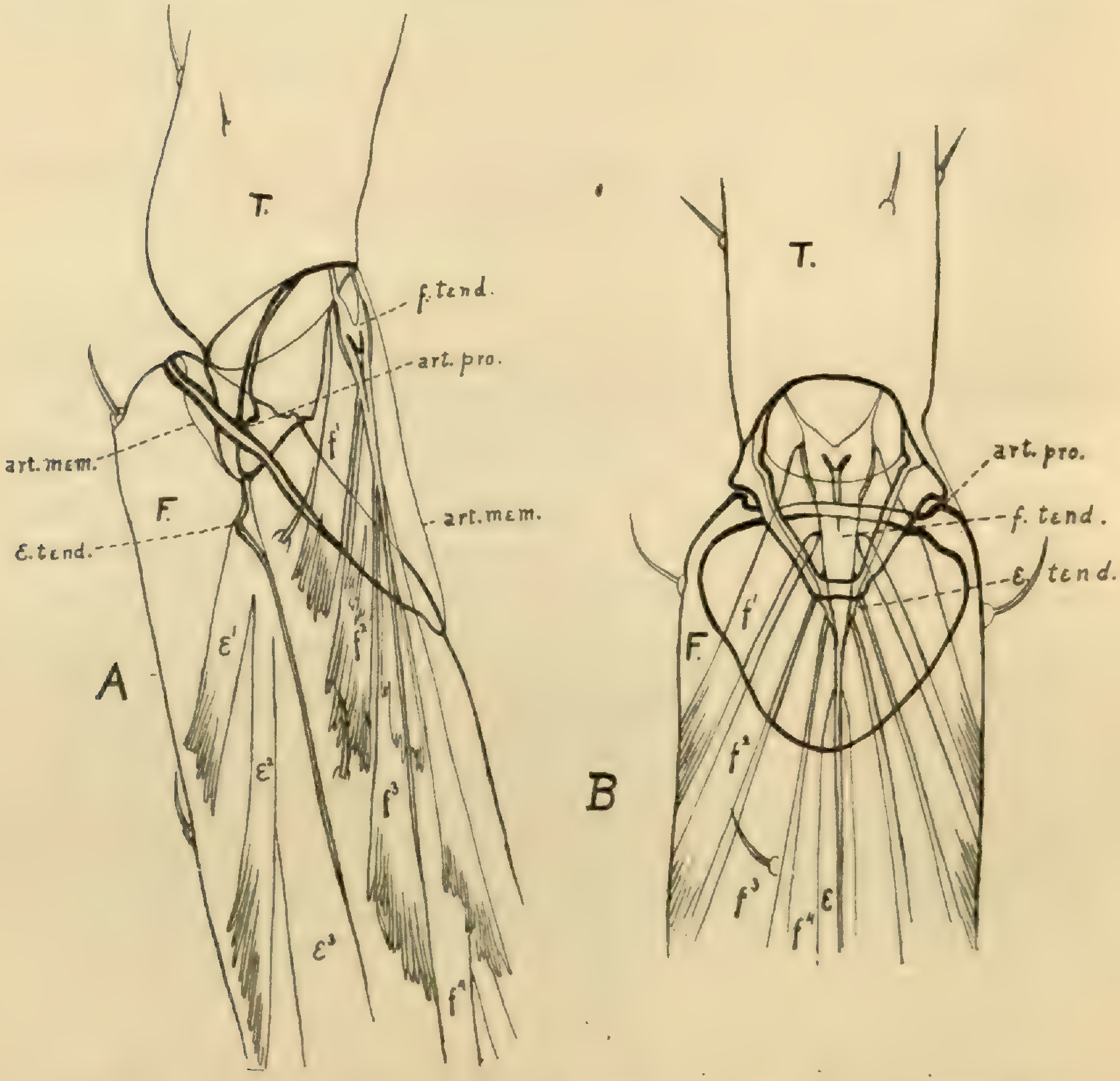

FIG. 1. The knee joint of *Aphis brassicæ*. *A*, side view; *B*, viewed from beneath; *T*, tibia; *F*, femur; *art.pro*, articular process; *e.tend*, extensor tendon; $e^1e^2e^3$, extensor muscles; *f.tend*, flexor tendon; $f^1f^2f^3f^4$, flexor muscles; *art.mem*, articular membrane.

of the femur when the leg is fully extended, but is all exposed when the leg is at extreme flexion. An articular membrane connects the extreme edges of femur and tibia, as shown in Fig. 1, *A*.

Beneath, the hard parts of both femur and tibia are deeply emarginated, exposing a broad articular membrane. When in extreme flexion the rims of tibia and

femur almost touch, and the articular membrane is drawn deep into the femoral cavity. The tendons find their attachment to the outer and inner sides of the rim of the tibia and, extending into the cavity of the femur, serve for the attachment of a series of muscles, as shown in Fig. 1, *A* and *B*.

The flexor tendon in the earlier stages is only a V-shaped thickening of the articular membrane, but later the point of the V extends deeply as an internal pocket for the attachment of muscles reaching nearly to the base of the femur. There are two sets of muscles attached to this tendon, extending obliquely to the right and left sides of the femur. The first of these, f^1, in the figures lying at about 45° to the long axis of the femur, and the others marked f^2, f^3, etc., lying more nearly longitudinally.

The extensor tendon attaches to the dorsal rim of the tibia by a broad ribbon-like portion and soon expands into a broad plate at right angles to this first portion and then

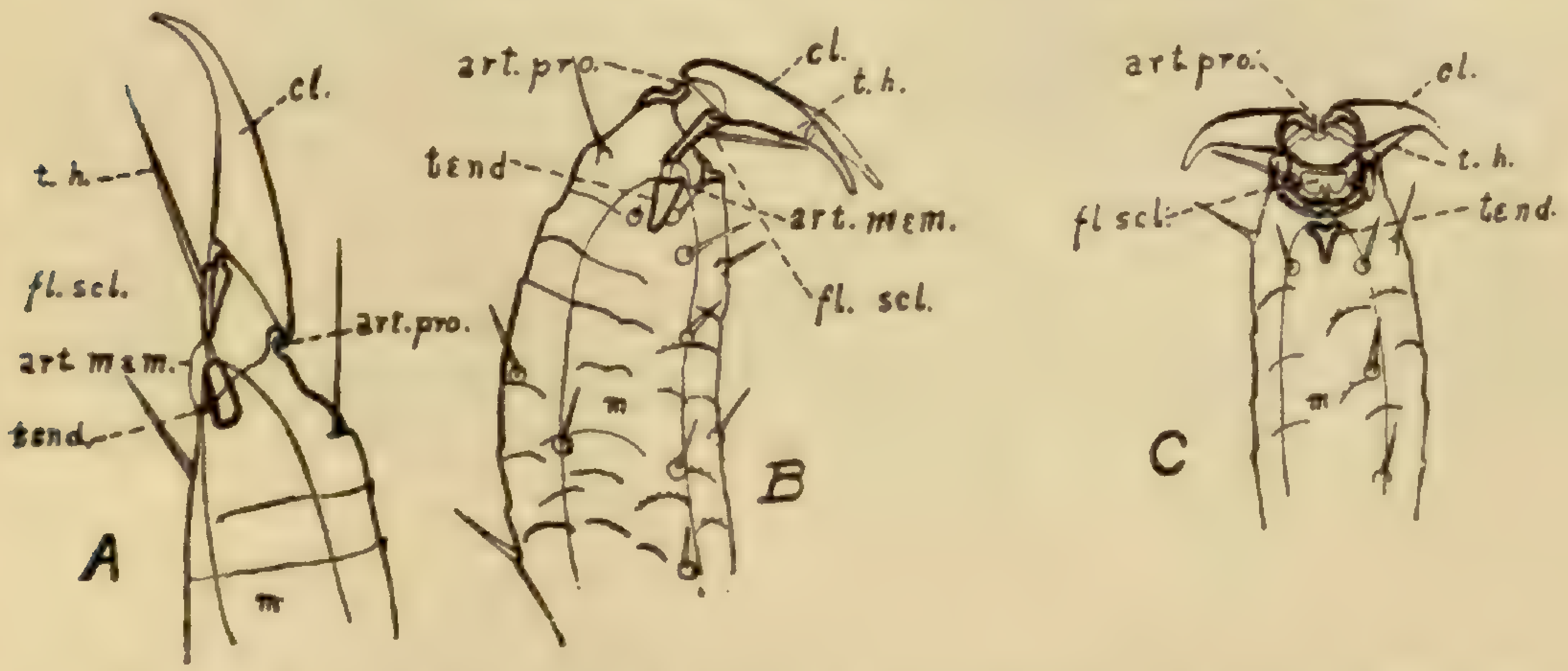

FIG. 2. End of foot of *Aphis brassicæ*. *a*, side view of claws at extreme extension; *b*, *Ibid*, claws flexed; *c*, viewed from beneath; *cl*, claw; *t.h*, tactile hair; *fl.scl*, floating sclerite; *art.pro*, articular process; *art.mem*, articular membrane; *tend*, tendon; *m*, muscle.

narrows to a ribbon and extends deeply into the femur even in the earliest stages. A short muscle, *e*, is attached to the disk, followed by a series of others, somewhat as the flexor muscles are arranged, only that there is but a single series, finding their attachment to the middle dorsal side of the femur. Tendons are first developed as somewhat tubular processes, but always collapse after the

molt so that the tubular character can never be made out. In the case of the extensor tendon of the knee the enlarged disk must require a considerable stretching of the portion of the tendon further out to enable it to pass.

The tendon of the claw is very short up to the last molt in the case of plant lice. The structure at the end of the last tarsal joint is shown in Fig. 2. At the extreme end of the foot there are two processes over which the base of the claws rotate. The only other attachment aside from the soft articular membrane is a median floating sclerite capping the larger part of the end of the cavity of the foot and which bears the tactile spines extending forward below the claws. This floating sclerite in other insects forms the base of the empodium and pulvillæ. Neither of these is present in the case of the plant lice unless the soft skin immediately beyond this sclerite be so designated. The lower edge of the margin of the cavity is a strongly developed ridge upon which the internal tendon bears when the claws are extended, and against which the floating sclerite rests in extreme flexion. On either side of this thickened and elevated ridge there is a distinct notch allowing considerable lateral motion of the sclerite. The posterior ridge of this floating sclerite extends inward as two processes joining with the two wings of the heart-shaped tendon. The tendon proper is entirely internal as is shown in the figure, and the muscle fibers are attached to all sides. The other attachment of the muscle is to the base of this large second joint of the tarsus.

There are really no true tendons in insects; *i. e.,* the tendons of the legs are only such in a physiological or morphological sense, and not at all in structure or origin, but belong instead to the class of internal processes which includes the well-known internal skeleton or the head and thorax, the tendons of the jaws in mandibulate insects, the great internal disk-like tendons for the attachment of the elevator muscles of the wings in the Odonata, and the skeletal and tendonal process of the ovipositor. The

only difference between a skeletal process and a tendon is that one is invaginated from a relatively fixed part of the body and the other from a moving part. While insect tendons are, therefore, not homologous with the tendons of vertebrates, it is probably wise to retain the name just as in the case of femur and tibia for parts of the leg, where likewise there is no homology with the bones of vertebrates where the names primarily apply.

ABNORMAL INCISORS OF MARMOTA MONAX L.

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The common woodchuck or ground hog, *Marmota monax,* is found rather frequently in most parts of central Kentucky; and, since it occupies the same burrows, or others in the immediate vicinity, generation after generation, it is not uncommon to find in these regions portions of their skeletons, skulls, vertebræ, teeth, etc., in the neighborhood of their habitations.

Fig. 1. Skull of *Marmota monax* L., right incisor removed. Natural size. Photograph by Spengler, Lexington, Ky.

The interesting specimen which is illustrated here was found near Silver Creek, Madison Co., Ky., by Mr. Charles Meeks, who presented it to Mr. Thomas Goff, of Lexington, Ky. It has recently been given to the Museum of Transylvania University. The upper incisors are extremely long and curved so as to form with the parts imbedded in the premaxilla more than a complete

circle. This is beautifully illustrated by Fig. 1, in which the right incisor has been removed from the jaw.

Both teeth are turned somewhat toward the right, so that the right one projects from the mouth; but the left incisor strikes the roof of the mouth to the right of the median suture, piercing the palatine plate of the maxilla

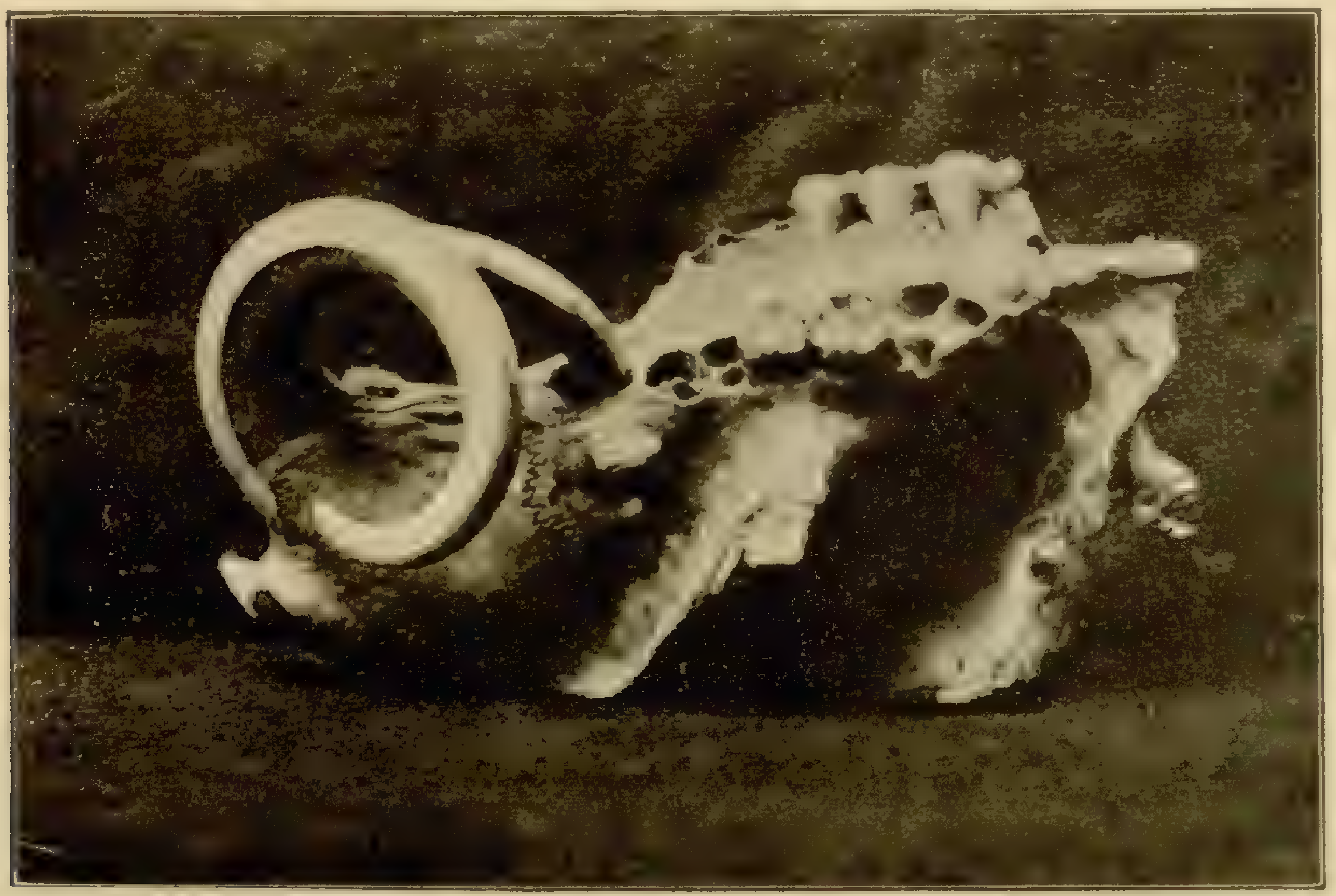

FIG. 2. Skull of *M. monax* L., with left incisor piercing palatine plate of right maxilla. Natural size. Photograph by Spengler, Lexington, Ky.

(Fig. 2) and extending through it to a distance of about 5 mm. The left tooth is not as long as the right one, its growth having been retarded, perhaps by the hardness of the bone it penetrated.

The manner in which the teeth of *Marmota monax* grow is familiar to all who know the Rodentia. The rodents all have a diphyodont dentition, that is, there are two sets of teeth, a temporary or deciduous set, and a permanent set. But the permanent teeth never cease to grow. There is a persistent pulp at the base of each tooth, which grows throughout the life of the individual.

Ordinarily the corresponding teeth of the upper and lower jaw oppose each other perfectly, and the growth from the pulp only compensates for the amount worn off by biting. The incisors have a heavier coat of enamel on

the anterior portion of the tooth, and the more rapid wearing of the posterior edge keeps these front teeth chisel-like and sharp.

The abnormal growth of the incisors will occur whenever the upper and lower teeth fail to meet. An injury to either jaw, as for instance a bullet wound, might destroy the perfect opposition of the incisors. But the teeth in this specimen are sharp pointed and not worn at the distal end, as they would be if they had ever functioned properly, which fact would indicate that the wound must have occurred before the permanent teeth appeared.

A careful examination shows that the abnormality can be accounted for in another way. The socket of the left incisor is not normal in its position, and the tooth itself grows inward toward the right incisor, striking it about 8 mm. from the jaw. The latter tooth has on its inner side a groove extending from near the distal end to the point where the two incisors are in contact. This groove was produced by the pressure of the left incisor upon the right, and this pressure is undoubtedly the cause of the failure of both teeth to meet the lower ones. The abnormal growth then depended primarily upon a congenital abnormality in the position and direction of the socket of the left incisor. One of the lower teeth of the same skull was found, but has been misplaced. Mr. Goff informs me that it also was curved and much longer than usual.

It would be of interest to know how the animal with this curious set of teeth obtained food sufficient to prevent starvation. It may well be that this abnormality was the chief determining factor in its struggle for existence.

A NOTE ON THE COLORATION OF PLETHODON CINEREUS

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On September 9, 1905, Mr. A. A. Allen found, near Buffalo, N. Y., a salamander[1] 6.5 cm. long which was, at first sight, believed to be a small *Spelerpes ruber*, but closer inspection proved it to be otherwise. The head, sides and back are of uniform coral red, gradually fading into pinkish on the immaculate belly (Fig. 7). The sides and the dorsum of the distal half of the tail are heavily mottled with black, leaving the dorsal line of the proximal half the same color as the body. The mottling extends upon the ventral side of the tail, but the spots are here much lighter so that the general pink color of the under parts is evident. On the right side the black blotches of the tail begin immediately behind the leg, while on the left the base of the tail is an immaculate red for some distance behind the leg.

This specimen was found under a piece of bark in a dry and rather open woodland. About three weeks later in a nearby locality there was found a second specimen which upon comparison proved to agree in all essential respects of coloration with the first. This one escaped before it was killed and preserved.

On April 27, 1907, near Beesemer, N. Y., a short distance south of Ithaca, Mr. Allen found another specimen[2] (Fig. 6) which is identical in form and similar in coloration to those taken near Buffalo. The Beesemer specimen is a carrot red with a cluster of minute black dots on the top of the head and a row of similar dots along the sides of the back in a position which corre-

[1] No. 5,047 Cornell University collection.

[2] No. 5,048 Cornell University collection.

sponds to the dorsal portion of the black lateral band in *Plethodon cinereus erythronotus.* This row of dots is broadest above the region of the arm, whence it is gradually reduced as the leg is approached. The coloration of the tail is similar to that of the Buffalo specimen excepting that the black color, instead of being collected in blotches, is more diffuse and continuous with the same color in the trunk region.

When these specimens were examined more closely they were found to have the body proportions and all of the structural features of *Plethodon cinereus.*

In the Cayuga Lake Basin both *Plethodon cinereus cinereus* and *P. c. erythronotus* are abundant and great variation with regard to coloration has already been noted. Several hundred specimens, mostly from this region, were examined with a view to determining the extent of the variation in coloration. This resulted in the selection of a series of fifteen individuals, of practically the same size, which show a fairly complete transition, in regard to coloration, between the typical *Plethodon cinereus cinereus* and the red forms taken near Buffalo. The middle of the series is occupied by a typical *P. c. erythronotus* (Fig. 4). From this variety the coloration in one direction grades into *P. c. cinereus* and in the other into the red form.

Cope[3] describes the variety *erythronotus* as follows:

"A broad light-reddish stripe commences at the nape of the width of the interorbital space, and continues to the tip of the tail, on which it diminishes gradually in width. The central region of the stripe generally exhibits a very fine mottling of brownish, scarcely obscuring the effect of the red ground. The mottling is sometimes equally distributed—sometimes concentrated in some places more than others. The sides of the body are abruptly and continuously dark brown, but soon fade off below into the pepper and salt of the lower sides and belly. . . . The color of the red stripe varies considerably. Sometimes it has a shade of pink—sometimes of orange or yellowish."

In all individuals examined from this region the red dorsal stripe on the tail grows narrow very rapidly. The

[3] Cope, E. D., "The Batrachia of North America," Bull. 34, U. S. Nat. Mus., p. 135.

distal third is mottled so heavily with black that the stripe, as such, is lost. The large number of specimens examined indicates that the typical *P. c. erythronotus* is not more common here than the red intermediates.

The transition between the variety *erythronotus* and the red form is accomplished thus: the red dorsal stripe first extends cephalad covering the whole top of the head where there is found in all intermediates a sprinkling of brown dots (Fig. 5). It then invades the sides of the head passing to the snout underneath the eyes. From this position it spreads in all directions, replacing the brown until the whole body is thoroughly suffused with red. In such specimens the brown color-pattern is evident but subdued by the red tone due to the invasion of this color into the whitish areas between the clusters of brown blotches.

The further transition consists in the expansion of the red ground-color and the gradual reduction of the brown blotches which persist longest on the top of the head, along the dorsal abrupt border of the lateral band, down the middle of the back and on the tail. In the Beesemer specimen only the vestiges of the brown markings remain in the regions just mentioned. On the limbs the invasion of red proceeds from the base towards the extremity, the brown markings showing longest upon the hands and feet.

In the Buffalo specimen the brown markings are everywhere apparently obliterated excepting upon the tail, the snout and the region between the eyes and a cluster just behind and below the left eye. In the alcoholic specimen there are revealed, along the sides of the back in the shoulder region, very fine specks of brown pigment arranged in a narrow band which can be traced to the leg region, although the dots are faint and much scattered in the caudal half, and in the living specimen did not show at all.

According to Cope[4] intermediate specimens between

[4] Cope, *op. cit.*, p. 136.

the varieties *erythronotus* and *cinereus* are uncommon, for he says:

"Among the very great numbers of specimens which I have examined in the collections of the Smithsonian Institution, The Academy of Natural Sciences and Essex Institute I have observed but four specimens of the red-banded variety and four of the gray which could be regarded as intermediate in character."

In the material at hand I find that the intermediate individuals, between the varieties just named, are fairly numerous; so that a series was selected which forms almost an insensible transition from the one to the other. The method here is exactly the reverse of that described above in connection with the red forms; *i. e.*, the red is replaced by brown. In describing the intermediate specimens which he studied, Cope outlined the method which I find carried out in detail in my material. He writes:

"This [the intermediate character of his specimens] appears in a rufous cast in the dorsal color of the latter [variety *cinereus*] and a slight obliteration of the borders of the dorsal band in the former [variety *erythronotus*]."

The brown of the lateral band in *P. c. erythronotus* begins first to encroach upon the red of the dorsal stripe so that its edges become scalloped (Fig. 3). This spreading of the brown color continues until the dorsal stripe is heavily blotched and the red becomes very dull (Fig. 2). Then the brown blotches gradually coalesce, in consequence of which the red stripe, as such, is obliterated, yet enough of the red pigment remains to give the effect of a dull liver-brown to the back of *P. c. cinereus.* In a number of specimens of this variety all traces of liver-brown have disappeared, rendering the back uniform in coloration with that of the sides (Fig. 1).

In respect to structural characteristics no variations were detected except in the case of one red intermediate where only seventeen costal grooves were present. The body proportions of this individual were slightly less than the others.

Data bearing upon the relation of this variation to environment, food, moisture, etc., are entirely wanting. The red specimen taken near Buffalo was at an altitude of 1,000 feet above sea level. That near Beesemer, 800 feet. Individuals kept in the terrarium under entirely different conditions than those from which they were taken in nature never change in coloration so far as I can determine, which indicates that the variation is independent of the nervous system. The age of the individual seems to have no relation to variation. Among adults of all sizes the different intermediate forms are found. There are in the collection of Cornell University about a dozen specimens taken soon after transformation. They are all typically of either the variety cinereus or erythronotus except one which varies decidedly towards the red form.

EXPLANATION OF PLATE.

FIG. 1. *Plethodon cinereus cinereus* in which all traces of the dorsal stripe have disappeared.
" 4. *Plethodon cinereus erythronotus.*
" 6. The red specimen taken near Beesemer, N. Y.
" 7. The red specimen taken near Buffalo, N. Y.

The other figures, according to their position, are intermediates between *P. c. cinereus, P. c. erythronotus* and the red Buffalo specimen.

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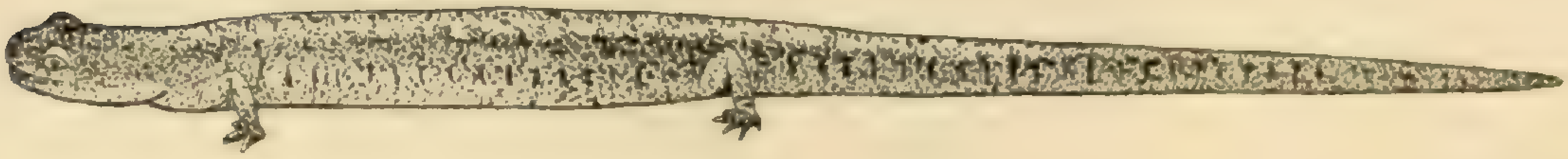

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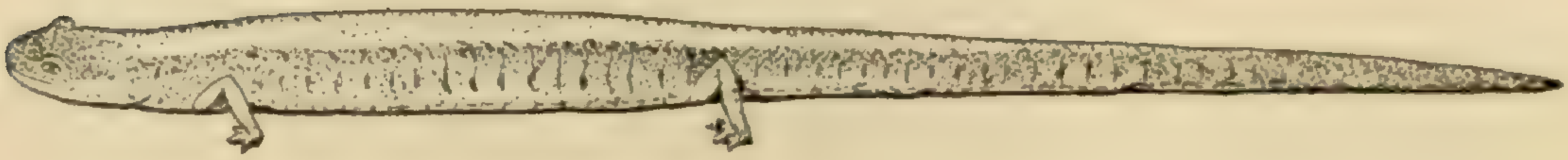

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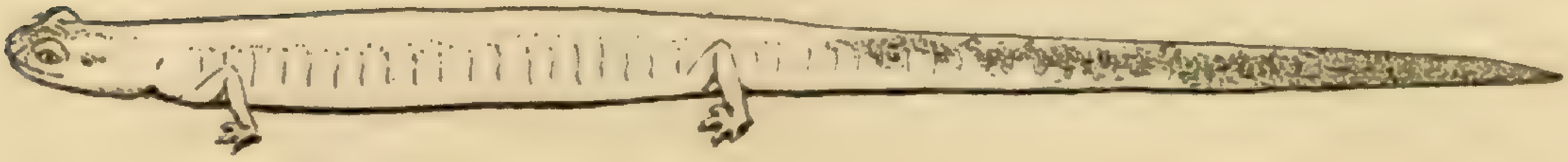

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A.G. Hammar, del.

SOME EXPERIMENTS ON THE ORDER OF SUCCESSION OF THE SOMITES IN THE CHICK

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THE experiments described in the present paper were performed at the University of Chicago during the year 1903-04, under the direction of Professor F. R. Lillie, to whom thanks are due for much advice and suggestion. In the course of the preparation of the data for publication during the last summer I learned that another investigator, Mr. J. Thos. Patterson ('07), had hit upon the same problem, and his results appeared before this article could be published. It has been suggested, however, that the work described may be of value in confirming Mr. Patterson's conclusions.

The problem, suggested by Professor Lillie, was the investigation of the statement, so generally made by embryologists, that, in the chick, somites arise in front of the one which is formed first. An examination of the most important of these statements will make clearer the nature of the problem. The estimates of von Baer ('28) and His ('68) did not require serious consideration, for they were not based upon a close study of this point. That of Kupffer and Benecke ('79), who thought that three or four somites arose in front of the one which first appeared, was founded upon an examination of a rather wide series of embryos, but only in surface view. Miss Platt's ('89) work rested upon a study of sagittal sections, and as it was altogether a careful examination of the subject, my attention was directed particularly to her conclusions. Briefly, her account of the formation of the somites is as follows:[1] The first cleft divides two

[1] *Loc. cit.*, pp. 177, 178.

forming somites. The somite behind the cleft is called the first one in the series. The one anterior to it, protovertebra *a*, forms slowly, while four or five are making their appearance behind. After five or six somites are visible in all, another, protovertebra *b*, arises slowly in front of *a*. Protovertebra *b* is said to be rudimentary, never becoming completely cut off from the mesoderm in front.

It will be noted in this account that although two somites are described as arising in front of the one first formed, in reality there is but one to be considered—protovertebra *b*—for protovertebra *a* makes its appearance at the same time with the one behind it. An examination of Miss Platt's sections[2] would lead one to agree in the main with her account of the order of formation of the somites, except in regard to the appearance of protovertebra *b*, whose growth has to be followed in a series of sections from different embryos at successively older stages. The difficulty of identifying a growing somite in this way casts much doubt upon even its existence, and it was to test the question therefore that these experiments were devised.

The aim of the experiments was to mark or destroy, in embryos with a small number of somites (not more than five or six) the most anterior somite on one side, and so to determine whether any more were later formed in front of this. The ideal stage to have secured would have been that of an embryo with only a single pair of somites, but repeated failures to obtain this condition verified the statement made by Miss Platt,[3] founded upon a study of sections, that the first cleft occurs between two forming somites. An operation, then, even as early as at the time of the first cleft would have had to take into account the first two pairs of protovertebræ.

The methods employed in the experiments were in general similar to those used by Mr. Patterson. For open-

[2] *Loc. cit.*, Plate I.

[3] *Loc cit.*, p. 177.

ing and sealing the egg Miss Peebles'[4] method was followed. For destroying the somites two fine depilatory needles, ground to a hair point on an oil-stone, were used, one, at the negative electrode, touching the albumen, the other, at the positive electrode, serving to prick the somite which was to be marked or destroyed. For the current four Samson dry-battery cells, each with an electromotive force of 1.5 volts, were connected in series. To prevent infection the instruments were sterilized in a flame. With this method of disinfection, 15 out of 84 embryos, or 18 per cent., were lost, but as the loss was occasioned by the sticking of the blastoderm to the shell, it can not be stated that it was not due in part to causes other than bacterial infection. A Zeiss dissecting stand was used for the operations, with lenses magnifying six diameters, and whenever possible the work was done with the bright sunlight shining in upon the blastoderm. So great is the variation in distinctness of embryos at this early age, that even with the best of light the somites could not, except in a comparatively small number of cases, be counted with certainty. In the embryos, however, which were distinct, there was no room for doubt as to their exact condition at the time of the operation.

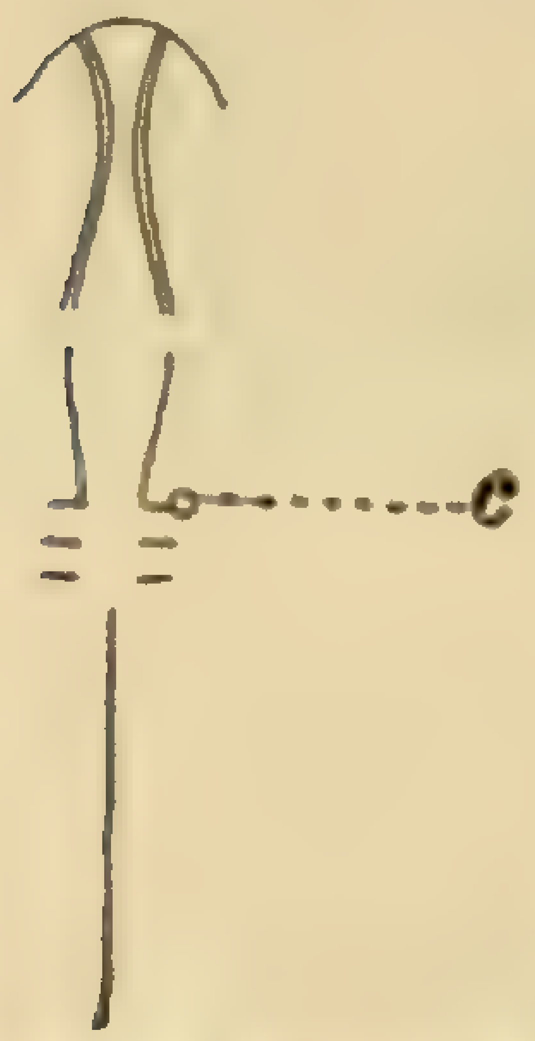

FIG. 1. Embryo 50. Sketch made at time of operation. c = place of operation.

From several experiments, the results of which furnish evidence for the solution of the problem, the following case has been selected for description:

Number 50 was operated upon after 30 hours of incubation. The operation was performed with the sun shining in upon the blastoderm, the embryo was distinct, and its three somites were readily counted. Fig. 1 is a sketch made at the time, showing the place of the operation, in which, it was noted, the needle passed obliquely inward.

[4] *Loc. cit.*, p. 406.

Fig. 2 shows the same embryo after nineteen more hours of incubation. The heart was beating when the egg was opened. The embryo was preserved in picrosulphuric-acetic acid, stained in Conklin's picro-hæmatoxylin, and mounted in xylol balsam. The drawing was made with the aid of the Abbe camera.

The first right somite is noticeably smaller than its fellow on the left, there is no break between it and the mesoderm in front, and only the posterior part of it shows the radial arrangement of cells which is characteristic of the normal somite. The scar of the operation shows at the side. A deeper examination in this region reveals, mediad of the scar, a clear area extending into the limits of both the first and the second somite of that side, indicating that the injury reached inward from the point of entrance of the needle. The second somite is also incomplete on its dorsal antero-lateral corner, as shown in the figure. Except for these injuries and the bend to the right which may have been caused by the operation, the embryo appears normal, the break in the neural tube at the anterior end being the result of pressure of the cover-glass.

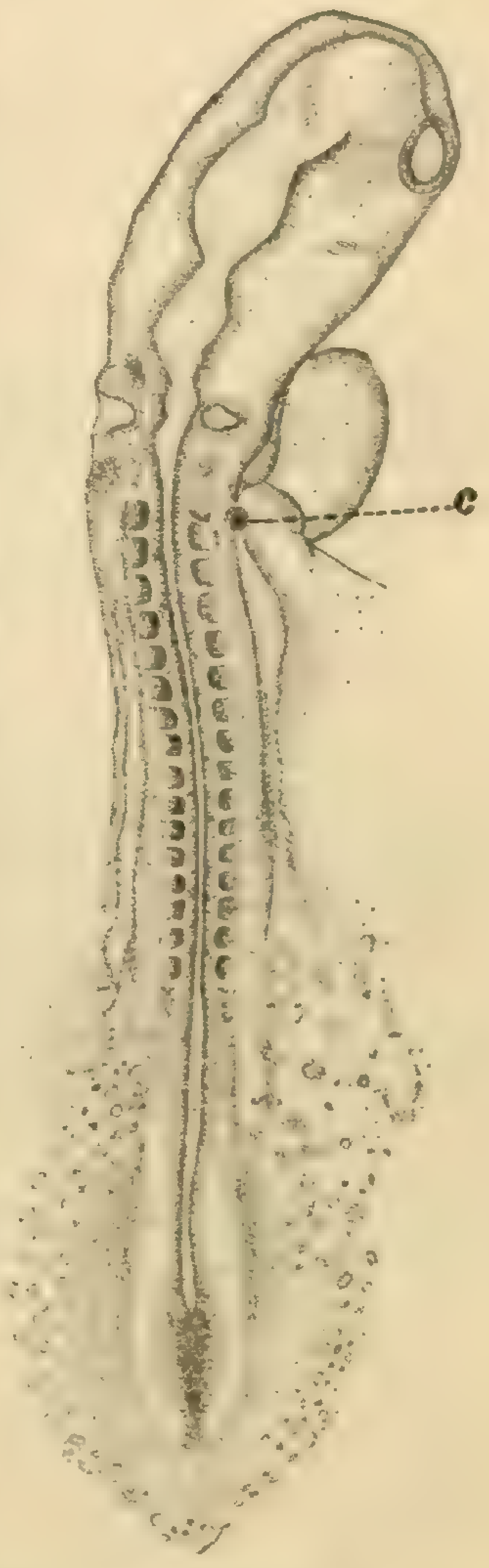

FIG. 2. Embryo 50, incubated 19 hours after operation. *c* = scar of operation. ×20.

Whatever else this experiment proved, it showed clearly that not more than two somites could arise in front of the one which is first formed. This of course shut out at once the hypothesis of Kupffer and Benecke, who assumed that three or four somites are probably formed in front.

Applying Miss Platt's description of the order of ap-

pearance of the somites to this case, it would seem that this embryo must have had the first of the two anterior somites, protovertebra *a*, already partly formed, at the time of the operation, and that there should, therefore, have been one more, protovertebra *b*, to arise in front of this. But no such somite appears in Fig. 2, and its absence led to the conclusion that there is no such somite as protovertebra *b*, in other words, that but one somite is formed in front of the first cleft which appears. The simplest explanation of Miss Platt's error is that she mistook protovertebra *a* in sections of older embryos for protovertebra *b*. This is much more probable than that she could have mistaken, as Mr. Patterson suggests,[5] the most posterior transitory shallow depression in the head mesoderm for the first cleft.

If it be objected that the experiment does not prove that one or two somites may not arise in front of the one first formed, it may be said that if they do arise, the rate of their formation, compared with the rate of formation of those that appear behind, is contrary to the description of this process by Miss Platt,[6] according to whom the rate of formation is much greater behind the first formed somite than it is in front. Either then somites are not formed in front, or, if they do arise, the description of the rate of their formation is not correct.

In conclusion, then, this experiment, in proving that not more than two somites could arise in front, showed the inaccuracy of Kupffer and Benecke's estimate of the number formed.

It showed further, in regard to Miss Platt's work, either that her description of the time of formation of the somites was incorrect, or, if development proceeds according to her account, that no somites, except the rudimentary one, arise in front of the first cleft.

Thus the result of the experiments, with reference to the condition of the problem up to the time when Mr.

[5] *Loc. cit.*, pp. 129, 132.

[6] *Loc. cit.*, p. 177.

Patterson began his work upon it, was to throw the burden of proof on those who claimed that somites do arise in front of the one first formed, rather than on those who held that, in their formation, they obey the laws of progressive differentiation which govern the early development of birds.

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DWARF FAUNAS

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FAUNAS in which all the individuals are uniformly so small as to be notable for this reason are common both in recent and past times. Such dwarf faunas may be merely an association of normally small species; or they may be individuals much smaller than the normal size for that species, prevented for some reason from attaining full size.

The following is an attempt to summarize some of the principal recent and dwarf faunas with the probable causes producing them. It is confined to invertebrate, water-living faunas. The article is primarily a summary of such literature as chanced to be seen; that very much of importance was overlooked is undoubtedly true, but it is thought that the major causes of dwarfing are here noted.

The first part of the article is a discussion of the chief agencies of dwarfing using recent examples as illustrations; the second part considers a few fossil examples of dwarf faunas with their probable causes.

The following are the chief agencies of dwarfing as noted in recent and fossil faunas:

1. A change in the normal chemical content of the water.
   (*a*) Due to a freshening of the sea water.
   (*b*) Due to a concentration of the salt, iron, etc.
   (*c*) Due to an increase in H_2S and other gases.
2. Presence of mud and other mechanical impurities in the water.
3. A floating habitat.
4. Variations in temperature.
5. Extremes in depth of water.

1. *A Change in the Normal Chemical Content of the Water.*—Any change in the environment of an animal which is away from that best suited to its highest development tends to its deterioration. If a species develops best in normal sea water, then an increase or decrease in the chemical content of the water should be detrimental to the animal, and this detriment should be expressed in the shell, since, as shown by Hyatt and others, there is the most intimate relation betwen the soft and the hard parts of an animal, the least injury in the soft parts being immediately expressed in the growing shell. This expression will usually take the form of a dwarfing in size, thinning and smoothing of the shell or development of bizarre form.

The possible changes in the normal chemical content of the water are exceedingly numerous and all doubtless affect the animal to a greater or less degree. The following appear to be some of the more important of such changes which produce a dwarfing effect.

(*a*) *A Change due to Freshening of the Water.*—That many forms of animals find fresh water detrimental to them appears to be indicated by the fact that at present whole groups are excluded from it, as the Echinodermata, Brachiopoda, Cephalopoda, Tunicata, etc.

The many streams emptying into the Black and Caspian seas, make them fresher than the Atlantic Ocean. The faunas of these are typically marine, but practically all are dwarfed in size as compared with the same species in the Atlantic. For example, the following Black Sea species are considerably smaller in the Black Sea than in the British seas: *Littorina rudis, Cerithium adversum, Trochus umbilicus, Murex erinaceus, Nassa reticulata, Cardium edule, Anomia ephippium, Venus gallina, Tellina tenuis, Mactra triangula, Solen ensis, Pholas candida,* etc.[1]

The common European cockles, Cardium, are large, thick and rough shells, and thrive best under purely marine conditions. The species found growing in brack-

[1] Forbes, E. Nat. Hist. of European Seas, pp. 201 and 202.

ish waters are smaller than those in normal sea water. *Cardium edule* is found in the British Isles in harbors and high up tidal rivers, where the water gets brackish; its shell is modified, invariably reduced in size, thin, and with less strongly marked external characters. The ten species of Cardium in the Caspian Sea are all aberrant forms, all related back to *C. edule,* small, thin and smooth, with lateral or central teeth or both suppressed. So likewise with the cockles of the Black and Baltic Seas; in the latter the salinity is reduced one half by the water from the rivers.[2] The Greenland cockle lives in estuaries; it is no longer found in Europe but is very abundant in the Pliocene (Crag) of Suffolk and Norfolk, especially in the fluvio-marine portions. It is thin, smooth, almost edentulous, with rudiments of a single tooth in each valve in the young shells which finally disappear.[3]

Some forms, as Scrobicularia and *Mactra solida,* have become thoroughly adapted to a brackish water environment and attain their largest size there. But many, if not most species, which live in normal sea water and in brackish water are smaller in the latter, as is true of *Cardium edule, Mya arenaria* and *Littorina littorea.*

(*b*) *Change due to a Concentration of Salt, Iron, etc.*— When a body of water has become concentrated to a point where precipitation of its salt takes place, as is practically the case in the Great Salt Lake or entirely so in the Dead Sea, no life can exist in it. But from the normal sea water to this condition there takes place progressively a lessening both in the number of species and in the size of the individuals there present.

Many fossil dwarf faunas have been ascribed to this cause, as, for example, those of the Permian.

That even a comparatively slight concentration of the sea water may produce a dwarfing in its fauna appears to be indicated by the western Mediterranean species. Dana gives the amount of saline matter in the Mediterranean as 3.9 per cent. as against 3.6 per cent. for the

[2] Dana. Manual of Geology, p. 121.

[3] Forbes, E. *Loc. cit.,* pp. 211–215.

Atlantic.[4] De Lapparent[5] states that this western portion has a few of the Atlantic species but all of reduced size. A comparison of British and Spanish coast species gives the same result. *Haliotis tuberculatus*[6] is larger at Guernsey than on the Spanish coast. The difference of temperature between the two localities may be another factor in causing this dwarfing.

(*c*) *Change due to an Increase of* H_2S.—The presence of much of this heavy gas in an enclosed or partially enclosed basin would prevent the presence of living organisms and hence the only fauna which sediments deposited here could contain, would be free-swimming or floating individuals. This pelagic fauna contains besides fish, pteropods, and especially larval forms of almost every animal group. Thus the sediment of such an enclosed basin would contain small shells, embryonic in character, pteropods and a few fish. Andrussow[7] has shown that in consequence of the greater salinity and density of the deep water, the Black Sea shows only slight evidence of vertical currents. Such currents are apparent only to a depth of 125 fathoms, and hence only to this depth is there sufficient oxygen for the support of animal life. At a depth of 100 fathoms the separation of H_2S is observable, increasing in amount with the increase in depth. The separation of H_2S is regarded as due to the agency of microbes (Sulfobacteria) living upon animal remains of the free-swimming and floating forms of life sunk to the bottom. It is attributable in part also to the derivation from sulfates. Hand in hand with the separation and enrichment in H_2S is the diminution in sulfates in the sea water, the separation of the carbonates and of FeS. In the great depths of this sea the bottom is covered with black or dark blue mud in which are abundant remains of free-floating diatoms, fragments of quite young pelecypods, and minute grains of $CaCO_3$, and much FeS.

[3] Clarke. N. Y. State Mus. Mem., 6, 200.

[4] Manual of Geology, 4th ed., p. 121.

[5] Traite de Geologie, 5th ed., 1, 132.

[6] Forbes. *Loc. cit.*, p. 171.

2. *Influence of Mud and other Mechanical Impurities in the Water.*—Though the western Mediterranean contains a dwarf fauna, yet it is the eastern part which is especially so characterized. This is attributed by de Lapparent[8] to the presence in the water of the eastern basin of many very fine particles of solid matter (Nile sediment) which becomes deposited only very slowly. A similar cause apparently aided in dwarfing some of the faunas of the Windsor (Nova Scotia) Carboniferous, also those of the Cobleskill, Rondout, Manlius, Bertie, etc.

3. *Influence of a Floating Habitat.*—Forms which live attached to floating seaweed will tend to be small owing to the fact that the increased weight of the individual due to growth will cause its sinking with its attached seaweed before the attainment of large size. Hence only the smaller individuals would occur on the seaweed or in the sediment beneath. Fuchs has shown[9] that in the eastern, shallower part of the harbor of Messina, the sea is now filled with different kinds of algæ, densely crowded together. This seaweed thicket swarms with small mollusks, seeking here food and protection. Here are species of Rissoa, Trochus, Turbonella, Columbella, Marginella, Cerithium, Cardium, Cardita, Lucina, Arca and Venus, but they are throughout of smaller size than normal. This dwarf fauna is thus not the result of stunted growth but is very probably due to the fact that the algæ can not support large and heavy shells. Such dwarfing and also thinning of shells fastened to seaweed (giant kelp) Arnold[10] notes in the case of *Pecten latiauritus* var. *fucicolus* of the California coast. This in its floating habitat far from shore is not subjected to the shock of the breakers, and hence the shell not only remains thin but also gradually loses its ribbed ornamentation. *P. latiauritus* likewise grows attached to kelp but when near shore it is more strongly sculptured than when living in deeper and quieter waters.

[8] *Loc. cit.*, 5th ed., 1, 132.

[9] Walther. Einleitung in die Geologie, p. 33.

[10] U. S. G. S. Prof. Paper 47, p. 131.

The ability of mollusks to reproduce before the attainment of full size accounts for the perpetuity of such dwarfed species. Semper, in reference to oysters and fresh-water mussels, says on this point:[11]

"Where formerly really gigantic pond mussels were found, now only quite small ones occur; and it is well known that the European oysters are gradually becoming smaller. This results from the circumstance that both these mollusks are capable of reproduction while they are still quite small, and now never grow to their full size, because they are destroyed before they have accomplished their full growth."

A probable fossil example is the dwarf fauna of the Ohio Black shale.

4. *Variations in Temperature.*—The influence of temperature upon the size of the animal is well illustrated by an experiment of Semper:[12]

"I found by experiment that this animal (*Limnæa stagnalis*) when young first begins to assimilate food, and consequently to grow, when the water is about 12° C.; at the same time a temperature much below has no injurious effects on the animal's life, though it entirely prevents its growth. . . . Assuming that a young Limnæa were placed in a lake or stream of which the temperature constantly exceeds the minimum at which the snail can begin to grow, during only two months of the year, while it never perhaps reaches the high optimum 25°, the mollusk will be unable to attain its due proportions during the first year, or to grow to its full size even during the second, and thus a dwarfed form will inevitably arise. This dwarfed form will still be able to reproduce and multiply itself, for the maturation of germinal matter—the ovum and the sperm—takes place during the winter and early spring, at a time when the low temperature of the water hinders all growth. The optimum of warmth for sexual processes is much lower than that for growth. Thus a permanently diminutive race might arise if the conditions of temperature above described remained constant for several succeeding years in the lake or streams in which the young mollusks or the eggs have been deposited."

But not only does too low a temperature produce dwarfing but when the temperate or polar species are introduced into water warmer than their optimum, they likewise become smaller.[13]

[11] Semper. Animal Life as affected by the Natural Conditions of Existence. D. Appleton and Co., 1881, p. 425.

[12] *Loc. cit.*, pp. 108 and 109.

[13] Semper. *Loc. cit.*, p. 118.

Dall says:[14] "As in mammals and birds so in Pectens the same species in the northern part of its range is larger than in the south unless its habitat is distinctly tropical."[15] So too the slight excess of temperature, 3° within the Mediterranean over that of the Atlantic in corresponding latitudes may help to cause the dwarf fauna within that basin.

Möbius mentions[16] that the same mollusks living on the coast of Greenland and in the Baltic Sea are in the former very large and in the latter small and thin-shelled; this variation he attributes to the constant temperature in the former case and the very great extremes in the latter.

The dwarf faunas of the Black and Caspian Seas are doubtless partly due, according to Forbes,[17] to the great extremes in temperature which they experience between winter and summer.

5. *Change due to Extremes in Depth of Water.*—For each organism there are certain limits of depth of water in which it best flourishes; outside of these in either direction there naturally results a tendency towards pauperization.

(*a*) *Very Shallow Pools.*—Semper[18] took specimens of *Limnæa stagnalis,* hatched from the same mass of eggs, and placed them in aquaria containing different volumes of water. "All the animals were under equally favorable conditions" (as to food, temperature, gases, etc.) "irrespective only of the volume of water which fell to each animal's share; this varied at most between 100 and 2,000 c.c." The result showed that "the smaller the volume of water which fell to the share of each animal, the shorter the shell remained." The number of whorls was the same, four, but the average length of the shell in the 100 c.c. of water was ¼-inch, while in the 2,000 c.c. volume it was ¾-inch.

[14] Arnold. U. S. G. S. Professional Paper 47, p. 133.

[15] See also Weller, Pal. N. J., 4, p. 77.

[16] Semper. *Loc. cit.*, p. 132.

[17] *Loc. cit.*, p. 211.

[18] *Loc. cit.*, p. 161.

(These measurements were taken from the figures.)

(*b*) *Great Depths.*—The pauperization of faunas with increase in depth appears to be due primarily to the decrease in light, which is essential to plant growth, and thus indirectly to animal life. Secondarily it is due to the decrease in temperature, the increase in the heavier contents of the water, and the greater pressure with depth.

In Geneva Lake the deep fauna is small and sluggish while their surface representatives are larger and active.

In abyssal ocean faunas there are few mollusca, and these are small, translucent, and white, with few crabs and annelids, but many echinoderms and porifera.[19]

With decrease in size from higher to deeper regions there is further pauperization, evidenced in the loss of brilliant coloring and variety of pattern. In the Mediterranean the proportion of colored to uncolored shells at depths of 35 to 55 fathoms is 1 to 3; at 100 fathoms and over, it is 1 to 18.[20]

The very many dwarf or depauperate fossil faunas already noted in the literature are doubtless but a small fraction of those still unnoted. The causes which are active at present in effecting this result were very probably equally active during each year of each era somewhere upon the earth's surface; so that the total number of such examples must be very great. Some of the fossil faunas, as for example, that of the Genesee, consist of uniformly small species, a selective agency having discarded the larger ones; here no stunting of growth is apparent. In such other faunas as that of the Pyrite bed of the Tully horizon, all of the individuals are smaller than the normal individuals of those species, thus showing very decidedly the stunting effect of environment. In still other cases, such as the Tertiary deposits at Steinheim, only a portion of the species were affected unfavorably by the environment, becoming dwarfed in size or of a bizarre shape, while the rest of the fauna were of the normal size for the species.

[19] Heilprin. Geographical Distribution, p. 262.

[20] Forbes. *Loc. cit.*, p. 189.

The following few dwarf faunas are described in illustration of the preceding agencies:

a. Faunas of the Cobleskill, Rondout, Manlius and Bertie of New York.

b. Faunas of the Pyrite bed of the Tully horizon and of the Clinton iron ore.

c. Fauna of the Genesee and Ohio shales; Styliolina limestone of New York.

d. Fauna of the Windsor (Nova Scotia) Carboniferous.

e. Faunas of the Permian.

f. Upper Cretaceous fauna of New Mexico and southern Colorado.

g. Tertiary lake fauna of Steinheim, Germany.

h. Pleistocene ? fauna of the lower Hudson River.

a. The Manlius, Rondout and Cobleskill formations of eastern New York, as well as the Bertie of the western part of the state are conspicuous for their dwarf faunas. The cause was probably in part the greater density of the water and in part the presence of lime mud, making the waters impure mechanically. The section of the rocks at Howes Cave is as follows:[21]

Coeymans, a typical lime sand rock (calcarenite).

Manlius, a fully laminated lime mud rock (calcilutite) with occasional beds of a lime sand.

Rondout, lithology as in Manlius but more argillaceous in upper portion.

Cobleskill (Coralline), lithology about the same as Manlius.

(Slight disconformity.)

Brayman (upper Salina), possibly the equivalent of the Bertie of western New York. Shales gray to green with traces of gypsum. Many iron nodules.[22]

(Great disconformity.)

Lorraine.

Deposition was probably continuous from the Cobleskill to the Coeymans, as there is no evidence of a stratigraphic

[21] Hartnagel. N. Y. State Mus. Bull. 69, p. 1114.

[22] Grabau. N. Y. State Mus. Bull. 69, p. 101.

break. That some at least of these beds were deposited in shallow water and even exposed at times to the sun is shown by the presence of cross bedding, ripple marks, and mud cracks. As is usually the case, these faunas show more strongly their dwarfed condition when viewed as a whole than when distinct individuals are considered; for the reduction in size has not been very great in individual cases, but is shown slightly in nearly all of the forms. For example, *Whitfieldella nucleolata* is equally small in all three of the formations (Cobleskill, Rondout and Manlius); the Spirifers, likewise, are conspicuous for their small size, *S. corallinensis* and *S. eriensis* from the two lower horizons and *S. vanuxemi* from the Manlius. *Favosites precedens* is a small form of *F. helderbergiæ* found in the two lower horizons. The presence of a lime mud seems to indicate that the waters in which deposition took place was denser with alkalies than normal sea water, otherwise the mud would have gone into solution as is usually the case when limestone is eroded. Such abnormal conditions would have a dwarfing effect upon the individuals living there, as has been noted in the case of the Mediterranean. To this unfavorable influence would be added the mechanical impurities of the mud, for on account of the shallowness of the water, the mud would probably be kept by the waves in an almost constant state of suspension. The occurrence of these dwarf faunas between the periods of small exceedingly dense seas or lakes, depositing salt and gypsum, and the normal marine conditions of the Helderbergian is an additional proof of the greater-than-normal density of the water at that time.

b. An exceedingly interesting dwarf fauna is that of the Pyrite layer in western New York at the horizon of the Tully limestone, but where that stratum is otherwise missing. This fauna is very fully discussed by Professor F. B. Loomis.[23]

The layer is a more or less discontinuous deposit of pyrite, appearing as very broad lenses but not over 1 foot in thickness. It contains a fauna of not less than 45

[23] N. Y. State Mus. Bull. 69, 892–920.

species, few of which, though adults, are over 2 mm. in diameter. The fauna includes 1 blastoid, 15 brachiopods, 12 pelecypods, 6 gastropods, 2 pteropods, 7 cephalopods, 1 trilobite, and 2 ostracods. These have all, however, been dwarfed until their average size is only one fifteenth that of the same species in the preceding Hamilton. The cause of this dwarfing is suggested to be the presence of much iron in solution and the gases arising from the decaying vegetable and animal matter. "The iron in the water, as ferrous carbonate, was probably precipitated by the sulfuretted hydrogen" from the organic matter, and thus formed pyrite ($FeOCO_2 + H_2S = FeS + CO_2 + H_2O$).[24]

That iron in the water has a dwarfing effect was shown by experiments upon fishes and tadpoles[25] which in eight months had been retarded in growth from three to five mm. The same is apparently shown in the fauna of the oolitic iron ore of the Clinton beds; in these beds at Rochester, N. Y., the species have "an average of about one third the diameter of the same species in the beds just above and below."[26]

The same condition was noticed in similar beds in Kentucky.

The following list will give a general view of the average size of the dwarfed forms. Loomis gives the average measurement of each species.

Spirifer fimbriatus mut. *pygmæus* Loomis is shown to be one twenty-fifth the normal size of the species.

Nucleospira concinna mut. *pygmæa* Loomis is one fifteenth that of the species.

Tropidoleptus carinatus mut. *pygmæus* Loomis is one fifteenth.

Nucula lirata mut. *pygmæa* Loomis averages one tenth the size of the normal species.

Paracyclas lirata mut. *pygmæa* Loomis is only one twentieth.

[24] *Loc. cit.*, p. 920.

[25] *Loc. cit.*, p. 895.

[26] *Loc. cit.*, p. 895.

The same species of gastropods and cephalopods vary considerably in size, much more so than do the brachiopods.

Since "iron solution in water tends to settle gradually to the bottom, as was found in experimenting on the fishes . . . it is not surprising to find that the brachiopods, which are either sessile or lie on the bottom, are the most dwarfed."[27] The brachiopods are seldom one fifteenth the normal in size, nor do they vary much from this; while the gastropods and cephalopods, groups of greater freedom of motion often vary in the same species from one twenty-fifth to one half the normal size; those which evidently grew up in this iron water being much smaller than those which entered it when partly grown. "All of these fossils then represent cases of arrested development, with the understanding that the arrest is at no given point but all through the development."[28] It is thus a case rather of retarded development or bradygenesis.

These retarded individuals appear like the young of earlier Devonian types.

c. From analogy with the Black Sea deposit, Clarke[29] conceives that the black, very thinly and evenly laminated shales of the Genesee in western New York, with their dwarf invertebrate fauna and fish, with their abundant segregation of iron sulfide, limestone nodules, etc., are likewise the result of accumulation in waters of great depth and imperfect vertical circulation. Dr. Clarke notes the presence of surface ocean currents in this region. He thus interprets the Styliolina limestone, four to six inches thick, at the base of the Genesee in western New York, as essentially a pteropod ooze caused by the meeting of a cold northern current and a warm southern one bearing these pteropods. The cold current thus acted as a barrier to the northwest spread of these pteropods.

An accessory agent in the production of this dwarf

[27] *Loc. cit.*, 898.

[28] *Loc. cit.*, p. 900.

[29] *Loc. cit.*, p. 201.

fauna of the Genesee may have been the presence of a sargasso sea as suggested years ago by Newberry for a similar fauna in the Ohio black shales.[30] The Genesee and Ohio black shales, occurring from New York to Virginia and west to Kentucky and Indiana, contain throughout their whole extent some or all of the following small species: *Lingula spatulata, L. ligea, Schizobolus concentricus, Chonetes scitulus, Leiorhynchus quadricostatus.* These species are not only small, but also thin, the largest or last named being very frequently if not usually crushed through the pressure of the overlying sediment. This smallness and thinness apparently indicates a habitat for the living animals where they were not subjected to the shock of waves as are shore-living species.

d. At Windsor, Nova Scotia, a very fossiliferous limestone, of Carboniferous age, occurs between conglomerate, sandstone and a black shale of the same age below and coal measures of sandstone and coal above. The coal is seen in the Joggins region across the bay. The shallow water or terrestrial origin of the former set of beds is indicated by the predominance of the coarse clastic sediment, the presence of ripple marks, footprints and Lepidodendra. A similar origin accounts for the latter.

The fossils of these Carboniferous limestones show the effect of the unfavorable environment in which they lived at the time these limstones were being deposited. Brachiopods suffer most, being depauperate throughout the series, the pelecypods, though much dwarfed, suffer less diminution, while the cephalopods were the most resistant to the dwarfing agencies; *i. e.*, the more closely a species was confined to a particular habitat the more dwarfed were the resultant adult forms.

The uniformly small size of most of the species is attributed by Dawson to two causes:[31]

1. Variation in depth and content of the water as

[30] Williams. U. S. G. S. Bull. 210, 110.

[31] Acad. Geol., p. 284.

illustrated by one layer which is brown and impure, indicating deposition in shallow and turbid water. In this layer the brachiopods are especially small and depauperate. *Productus cora* rarely reaches one inch in diameter and the Rhynchonellas are minute. The pelecypods are very abundant but dwarfed.

2. The influence of the formation of the beds of gypsum and gypseous marls at the time these limestone reefs were growing. Dawson ascribes the formation of these gypsum deposits to chemical change produced on the calcareous beds and reefs by contact of streams charged with H_2SO_4. Such streams are easily accounted for by the volcanic activity known to have occurred in this region while the shell beds were growing. The great amount of CO_2 released in the change from calcareous carbonate to gypsum would surely render unfavorable the water in which these limestone-secreting animals were living.

e. De Lapparent attributes the depauperized fauna of the Mediterranean in part to the greater preponderance of CO_2 in the water of that sea over that of the Atlantic.

One of the most notable facts arising from a study of red strata is the very frequent total absence in them of all fossils and the often dwarfed and impoverished faunas of the associated strata of other colors. Such red beds are especially conspicuous in the rocks of the Devonian, Permian and Triassic eras. Geikie mentions that fossils are practically absent from the red strata of the Old Red sandstone of England, but abound in the gray or black.[32]

According to the same author[33] "the impoverished fauna of the Permian rocks of central Europe is found almost wholly in the limestone and brown shales, the red conglomerate and sandstone being, as a rule, devoid of organic contents."

In speaking of these same rocks de Lapparent[34] says that "in northern Europe the mollusks of the upper

[32] Textbook of Geol., 2, 1002.

[33] *Loc. cit.*, p. 1066.

[34] Traite de Geologie, 5th ed., 1, 1017.

Permian are always of small size as if they had lived in particularly unfavorable conditions.'' The cause he gives is that ''there was formed a series of interior seas, soon dried up and where the excess of saltness had the effect of injuring the development of the mollusks. These seas have left here and there important deposits of salt and gypsum.''

That this dwarfed fauna was not the normal, open-sea fauna of the Permian is noted by a comparison with the species of the Alps, the Mediterranean region, and India. While in northern Europe the predominating forms are pelecypods and brachiopods, with exceedingly few cephalopods, in these latter more normal regions, the cephalopods become very numerous and all are of a larger size.[35]

It is interesting to note the resemblance of the fauna of the Carboniferous of Windsor, Nova Scotia, to that of the Permian of northern Europe. According to the determination of de Verneuil[36] several species of brachiopods and pelecypods are common to the two regions, showing that similar conditions tend to bring about development along similar lines.

(In this connection Schuchert's discussion of the question—Is there a Permian system or only a Permian formation?—is enlightening.)[37]

f. The dwarf fauna of the Cretaceous strata of New Mexico and southern Colorado[38] occurs in sandy shales and shaly sandstones, accompanied by innumerable fragments of wood. Cross bedding is frequent. The majority of the shells are of normal size, but with these occur many others which are distinctly smaller than in other regions. *Lima utahensis* Stanton is here only one half as large and *Lucina subundata* M. and H. is also smaller than in Utah. *Ostrea anomioides* var. *nanus* Johnson is

[35] De Lapparent. *Loc. cit.*, p. 1067.

[36] Davidson. *Jour. of Geol. Soc.*, 1863, p. 160.

[37] *A. J. S.*, 22, 29–46 and 143–158, 1906.

[38] Stanton. U. S. G. S. Bull. 106. Shimer and Blodgett. *A. J. S.*, 25, 67.

a dwarf form of the species *O. anomioides* Meek. *Ostrea lugubris* Conrad is a small species resembling the large *O. blackii.*

A probable explanation of this fauna and its habitat may be drawn from Metzger's observations[39] upon that much-studied shell, *Cardium edule.* This upon the sand shoals of the ocean flats is small, while it attains its maximum size off the rugged coasts of Norway and Scotland. These Cretaceous strata with their sand, cross-bedding, much fragmentary wood, and a marine fauna indicate a shallow sea into which emptied some large river, a condition probably somewhat similar to that of the eastern part of the North Sea at present.

g. It often happens that while a portion of a certain fauna is dwarfed, the rest are of normal size. Hyatt[40] discusses an excellent example of this mixture of dwarf and normal forms from the Tertiary strata of Steinheim, northwestern Germany.

Into the Tertiary lake at Steinheim migrated four varieties of *Planorbis levis.* The descendants of these are divided into the progressive series or those which became larger and more robust, and the retrogressive or those which became smaller, less robust and distorted.

The dwarfing of the one series may be explained as a sapping of the individual's energy due to its being in an unfavorable environment. It is common to note signs of old age appearing immediately after a severe injury to the animal.[42]

In gastropods this is often indicated by uncoiling and rounding of the whorls, so that these may be looked upon as signs of weakness in the animal. Hyatt discusses the reason for this as follows:

"Among living animals it is a matter of daily experience to find some races incapable of enduring variation in the surroundings to which others readily accommodate themselves and even thrive under."[41]

[39] Walther. Einl. in die Geol., p. 32.

[40] The Genesis of the Tertiary Species of Planorbis at Steinheim. *Bos. Soc. Nat. Hist. Anniv. Mem.*, 1880.

[41] Hyatt. *Loc. cit.*, p. 16.

[42] Shimer. Old Age in Brachiopoda. AM. NAT., 40, 115.

"In the individual the effects are shown in the disturbance of the laws of growth, producing abnormal or premature weakness or in the natural exhaustion of the powers of growth causing senility. A wound and its results, whatever they may be, can unquestionably be so classified, since it is primarily a severe shock to the system which lays additional burdens upon the powers of growth and is usually followed if severe by retrogressive metamorphoses or premature old age . . . normal old age simply expresses the normal wearing out of the powers of vitalized tissue to sustain itself against the perpetual friction of existing physical surroundings. . . . When we compare these effects of unfavorable environment in producing distortion and decrease in size of the individual with the corresponding distortions and decrease in size of the retrogressive sub-series there is a certain similarity which leads to the supposition that the latter are also probably due to an unfavorable environment."[43]

h. At Storm King, about fifty miles above New York, was found in drilling a series of holes across the Hudson, an apparently dwarf fauna including only two species, *Mulinia lateralis* (Say), of which there are hundreds of specimens and *Trivia trivittata* Say, of which there are but few specimens in our collection.

(These fossils were obtained by Professor W. O. Crosby in February, 1908, and through his kindness these facts are presented.)

These were found in but one drill hole, though probably the same species are present in the others but passed unnoticed in the drilling. They occur 620 feet out in the river from the Storm King shore, 40 feet below the bed of the river, *i. e.*, about 120 feet below the present river or sea level at that point. The Hudson is brackish at this point and as far north as Poughkeepsie, as is evidenced by the absence of ice houses below Poughkeepsie. Whether in the present bed of the stream there are any marine forms growing was not ascertained. The heavier sea water might still come up in sufficient amount to furnish a marine habitat even under quite fresh surface conditions. This dwarf fauna in the abundance of *Mulinia lateralis* suggests Pleistocene age.

These two species live at present off the New England

[43] Hyatt. *Loc. cit.*, p. 15.

and New Jersey coasts, in normal marine or but slightly freshened water. An average-sized fossil specimen of *Trivia trivittata* is three eighth inch long with a greatest diameter of three sixteenth inch. An average size for those off the Massachusetts coast is two third inch by one third inch. The smaller specimen is less strongly ribbed and less nodose.

One of the larger of the fossil specimens of *Mulinia lateralis* measures five sixteenth inch by one fourth inch. The young shells off the coast are small, thin, with margins subequally rounded and beaks inconspicuous and nearly touching each other; this description applies to all of the Hudson River specimens. It does not seem probable, however, though possible, that so many shells could be gathered at random as was done by the drill without getting some adults. The more probable explanation seems to be that these fossil individuals were living in an unfavorable environment, a water less than normally saline, and through a consequent sapping of vitality, were not able to attain large size.

Summary

In the first part of the above discussion was given what appear to be some of the principal causes for the dwarfing of invertebrate water-living faunas; these were illustrated by present-day examples. In the second part a few fossil examples are described with a brief discussion of the probable cause of the dwarfing in each case.

The chief agency is apparently an abnormal habitat. A species, for generations used to an environment of sea water with a certain unvarying density, temperature, clearness and depth, would become so accustomed to that state of affairs that a change in one or more of the factors would affect it unfavorably. An unfavorable environment causes a greater expenditure of vitality in the continuance of life than does a favorable one. Hence after the maintenance of life itself, there would be less surplus energy left for growth. There would thus result a

tendency to smallness of size especially in those species having comparatively little vitality to start with. It could happen then that from this cause alone either all or but a few of the species of a fauna would become dwarfed.

The hard parts of the animal are so intimately related to the soft parts that whatever affects the soft parts is immediately impressed upon the building shell. Thus whatever ill or good conditions the animal is subjected to are expressed in the shell, as are moist and dry summers recorded by the annual rings of exogenous trees.

Two classes of dwarf faunas are noted: (1) Faunas where the individuals are of smaller size than that to which the species grows under normal conditions; this is the resultant of an abnormal habitat. (2) Faunas where all the individuals are small but of the normal size of the species; in this case some selective action has weeded out all the large and heavy species, leaving a dwarf but not stunted fauna. Dwarf faunas usually include representatives of both these classes.

Dwarfing shows itself in two ways:

1. An acquirement of old age characters by the dwarfed animal. Such old age characters as sluggishness, loss of external sculpture, teeth, etc., are very common in stunted forms.

2. A retention of youthful characters. That is, the animal's growth takes place so slowly, due to the abnormal environment that saps the vitality, that death overtakes it before it has passed through the youthful stage, and the animal develops no old age characters.

NOTES AND LITERATURE

ICHTHYOLOGY

Life History of the Eel.[1]—The waters of the northeastern Atlantic and of the adjacent North and Baltic Seas have been subjected in recent years to a most elaborate and continuous investigation, thanks to government subsidies and international cooperation. A coordinated study of the plankton and an investigation of the breeding habits and the young of the important food fishes and of their migrations and movements, have made up the large part of the ambitious program of this International Commission. In the allotment of the field it has fallen to the Danish Fisheries Bureau to undertake to complete our knowledge of the life-history of the common eel. Dr. Johs. Schmidt, with the aid of the Danish fisheries steamer *Thor* and Dr. Petersen's young-fish trawl, has added a new, and almost final, chapter in the solution of this mystery which has puzzled naturalists for centuries.

The suggestion of Dr. Theo. Gill in 1864 that the peculiar ribbon-like fish known as Leptocephalus was the larva of the Conger eel was subsequently verified by Dareste's (1874) anatomical comparisons and Delage's (1886) successful rearing of a Leptocephalus through its metamorphosis into the Conger eel. It remained for the Italian zoologists Grassi and Calandruccio to demonstrate in 1897 that the larva known as *Leptocephalus brevirostris* was in reality the young of the common European eel, *Anguilla vulgaris.* Their conclusions were based upon anatomical comparisons, transitional stages, and experimental rearing of the larval Leptocephalus to the young Anguilla. Most, if not all, of the material upon which the work of the Italian investigations were based was obtained at or near the Straits of Messina where the famous whirlpools bring to the surface the organisms of the deeper waters.

The eel fisheries of northern Europe are widespread and in places, especially in the Baltic Sea, they are extensive. There were in 1881, 18,491 eel traps in operation along the Swedish

[1] Contributions to the Life-History of the Eel (*Anguilla vulgaris* Turt.). By Johs. Schmidt. Conseil Perm. Intérnational pour Expl. de la Mer. Rapports et Proces-verbaux, Vol. 5, pp. 137–274, Pls. 7–13.

coast, and in 1900, 22,608 in Danish waters, excluding fresh water and the smaller areas of salt water. Yet in spite of these extensive fisheries and the wide distribution of the eel along the coasts of the Atlantic and its tributary waters in Europe, absolutely nothing has been known of the spawning grounds, or breeding habits of the eels of these more northern waters. Sexually mature eels have rarely, if ever, been taken. Dr. Schmidt records the discovery of but a single sexually mature male eel of the silver (migrating) type in shallow waters off the coast of Denmark. Leptocephalus larvæ belonging to the common eel (*L. brevirostris*) have never been taken, until recently, in the Atlantic. The specimen taken by the Challenger Expedition in the North Atlantic and referred by Günther to this species proves upon reexamination to belong to another species having 140 myomeres instead of the 111–118 characteristic of *L. brevirostris*.

In 1904 a single example of this latter species was captured by Dr. Schmidt in the tow nets of the *Thor* west of the Faeroes, and a few months later Dr. Holt, of the Irish Fisheries Bureau, took a second specimen west of Ireland. These captures gave the clue which Dr. Schmidt has most successfully followed. In the next two years Leptocephalus was discovered by Dr. Schmidt in large numbers in mid-summer to the west of the British Isles and France over depths of 1,000 meters. The transition stages between the hyaline pelagic larvæ in the Leptocephalus stage and the colorless "elvers" which have long been known along the northern and western coasts of Europe were also found by the *Thor* but at the close of summer and in the autumn. After a thoroughgoing investigation of these grounds and of the data regarding the movements and distribution of the young elvers along the coasts of Great Britain and continental Europe Dr. Schmidt comes to the following conclusions.

The common eel of northern Europe spawns in the Atlantic Ocean west of the British Isles and southward at least as far as the northern coast of Spain. The essential features of the spawning ground are (1) a depth of at least 1,000 meters and (2) a temperature at this depth above 7° C. This belt is a relatively narrow one along the edge of the continental shelf as it rises from the Atlantic basin. Leptocephalus larvæ have long been known in the Mediterranean and a much greater extension of the spawning grounds beyond the known limits to the south is not improbable. The Atlantic basin with its greater depths and lower temperatures appears to afford an effectual

barrier between the American and European eels (*Anguilla chryspa* and *A. vulgaris*). Eels of European streams approaching sexual maturity and migrating seaward must travel to the edge of the continental shelf to reach suitable spawning grounds. The Baltic and North Seas are too shallow, and waters to the west of Norway are deep enough but their temperatures are too low.

The eels, as they migrate, undergo a considerable change in appearance, passing from the stage known as the yellow eel to that of the silver eel, in which feeding is suspended, the digestive tract is shrunken and sexual glands show some enlargement. The direction of migration in the Baltic in the autumn is out toward the open sea. The paths of migration are usually parallel to the coast and in shallow water, though eels have been known to cross channels 60 meters in depth. The direction and rate of migration was worked out by Dr. C. G. Joh. Petersen, the director of the Danish Fisheries Laboratory, by means of marked fish. The rate of movement in the migratory season is about 15 kilometers per day. The eels in these shallow waters, where their presence is revealed by commercial fishing, are none of them sexually mature. Their further movements are unknown but the presumption is that they continue their course toward the open sea and to the edge of the continental shelf. A single capture in the English Channel twenty miles from land confirms this conjecture, as do also the captures made by Grassi and Calandruccio in the whirlpools at Messina, where occasional specimens of the common eel are brought to the surface, which differ materially from those taken in shallow waters. They are silver eels in which the breeding dress is further accentuated by darker color, the anterior border of the gill openings and the pectorals become an intense black, the eyes also become enormously enlarged and the sexual organs show greater maturity. Maturing eels have also been taken from the stomachs of the sword-fish and in the collection of Prince Albert of Monaco is a large eel taken from the stomach of the cachelot. These facts in conjunction with certain testimony on the part of fishermen suggest the possibility of a pelagic or bathypelagic habitat of the eel in its migration to the open sea.

The larvæ *Leptocephalus brevirostris* of the eel are true pelagic organisms, as is shown by their entire organization. Neither their structure nor their distribution indicates any relation to a bottom habitat. In life they are perfectly transparent

and are found in association with typically pelagic organisms such as Salpa, Cymbulia and Phronima, as well as the young of other pelagic or deep-sea fish, among which are five additional species of "Leptocephalus." They have also the leisurely movements characteristic of many pelagic animals.

The pre-Leptocephalus stages of the eel are as yet wholly unknown. The earliest season of investigation has been the month of May and at this time the pelagic larvæ are found during the day in greatest abundance in levels at a depth of about 100 m., but rise to the surface levels at night. This distribution of the youngest known stages leads Dr. Schmidt to surmise that the eggs of the common eel are bathypelagic, and that the larvæ as they develop rise to the upper levels.

The pelagic larvæ appear to reach the height of the larval stage of development in June and cease active feeding, but do not as yet show the regressive phenomena which characterize the period of metamorphosis. They have also reached their maximum larval size 75 (60–88) mm. Both upper and lower jaws are equipped with long slender grasping teeth. No pigment is found in the body except in silvery iris of the eye. The digestive tract at this time extends through about two thirds of the length of the body.

The larval stage is followed by a long period of metamorphosis during which the form of the body changes from that of a colorless ribbon-like band to the pigmented cylindrical type with differentiated head and tail. The pelagic mode of life is abandoned and the young eels or elvers adopt the bottom habitat in shallow coastal and fresh waters into which they have migrated from the open sea. This period of metamorphosis occupies the entire year or more, during which no food is taken. The body gradually decreases in size as the metamorphosis proceeds, diminishing from an average length of 75 millimeters in the high seas in June to 65 millimeters a year later in coastal waters. The digestive tract shortens during this period from two thirds to one third of the total length of the body. Mandibular and vomerine teeth appear and dermal sense organs develop about the head.

During this long period of metamorphosis the Leptocephalus larvæ migrate slowly from their habitat above the 1,000-meter line shoreward. According to the recent summary of observations published by Professor Gilson, they reach the coasts of Spain and Ireland in October–December, and the western coasts

of France and England and the eastern shores of Scotland in January–February. In March the tiny elvers swarm along the shores of the Netherlands, Denmark and Norway and continue to arrive there during the month of May. Danish waters and the western Baltic form the eastern limits which the eel reaches in the elver stage. Their farther migrations into the Baltic and up the rivers of northern Europe are accomplished during the period of rapid growth which now ensues.

The extensive eel fisheries of Europe thus depend upon the migratory habit of a true Atlantic deep-water fish which seeks

Metamorphosis of the Eel (*Anguilla vulgaris*).
Figs. 1–2, 1st stage (*Leptocephalus brevirostris*). Figs. 3–6, 2d stage. Figs. 7–8, 3d stage. Figs. 9–10, 4th stage. Figs. 11–12, 5th stage. Fig. 13, 6th stage.

fresh-water streams and lakes for its period of growth but returns to the deep sea to spawn. CHARLES A. KOFOID.

The Valves in the Heart of Fishes.—The following note by Dr. H. D. Semor, of the College of Medicine in Syracuse University, New York, on the valves in the heart of fishes should be put on record.

It may be noted that in the so-called ganoid fishes there is more than one row of valves and from these ganoid fishes are derived the herring-like fishes. Some of these, as Dr. Senior has noted, have two rows of valves. Others have but a single one as in ordinary fishes.

"With regard to the question of teleosts having a conus arteriosus provided with more than one row of valves: In addition to Albula[1] which has long been known to have two rows, I have found a conus with two rows of valves (each row having two cusps) in *Tarpon atlanticus*,[2] *Megalops cyprinoides*,[3] and in *Pterothrissus gissu*.[4] I think this list will prove to be complete, as I have examined, with a negative result, Elops,[2] Chirocentrus,[5] Chanos,[3] Dorsosoma,[2] Notopterus,[2] Pomolobus,[5] Alosa,[5] Brevoortia,[5] and Boas has examined Osteoglossum.[6]

"A well-marked or vestigial conus arteriosus with *one* row of valves only, occurs in Elops,[4] Hyodon,[5] Chirocentrus,[5] Chanos,[3] Notopterus,[6] Osteoglossum[6] and Dorosoma.[2] That it also occurs in other allied genera, I have little doubt. When I collect enough specimens, I intend to describe and figure the conus (or vestige) in a sufficient number to indicate its mode of disappearance." DAVID S. JORDAN.

PARASITOLOGY

The Hereditary Transmission of Germ Diseases.—The earlier views which favored hereditary transmission of germ diseases have been subjected for nearly half a century to careful scrutiny at the hands of bacteriologists and are now generally rejected. Experimental evidence has been furnished from many quarters that the supposed cases are due to a contamination of the offspring during transit through the maternal passages at birth, or

[1] Stannius. Bemerkungen über das Verhaltniss der Ganoiden zu den Clupeiden, insbesondere zu Butirinus Rostock, 1846. Boaz. *Morph. Jahrb.*, Bd. 6, p. 527.

[2] Senior. *Biol. Bull.*, Vol. XII, p. 146.

[3] Senior. *Biol. Bull.*, Vol. XII, p. 378.

[4] Senior. *Anatomical Record*, Vol. 1, No. 4, p. 82. (*Am. J. of Anatomy*, Vol. VI, No. 4.)

[5] My own notes, unpublished.

[6] Boaz. *Morph. Jahrb.*, Bd. 6, p. 527.

occasionally to infection *in utero*, although in the majority of cases the cord and placenta form a barrier to the transmission of bacteria. Even when the bacteria gain entrance into the fetus there is no adaptation to the reproductive process.

Until very recently the part played by animal organisms in the transmission of diseases has been regarded as of very minor importance, and for the few known instances the same view rules with reference to conditions of transmission as already noted for bacteria. In the case of malaria, the oldest known protozoal disease, many experiments have been made to determine the occurrence of transmission *in utero*, from mother to offspring, and not only the general facts but also the details have been established.

A long series of able investigators, among them our own W. S. Thayer, have found that the malarial organisms present in the maternal blood do not occur in the blood of fetus and of the new-born. It has been generally agreed that these hæmatozoa can not traverse the placenta from the pregnant mother to the fetus. Moreover Bignami et Sereni demonstrated that the fetus lacks not only the parasites, but also the anemia which often characterizes the mother. The subject has been subjected to most careful reexamination at the hands of two Greek investigators.[1] In every case the maternal blood contained malarial parasites in greater or less abundance. In blood taken from the maternal face of the placenta, parasites were abundant, in that from the opposite or fetal face they were absent or very rare. In blood taken from the umbilical cord and from the liver, kidney and other organs at autopsies, not a single parasite was demonstrated. Thus they confirmed absolutely the view that these haematozoa do not traverse the placenta.

An interesting departure from these conditions is afforded by recent investigations on other disease-producing protozoa. The experiments are not extensive and in some cases contradictory. Thus Massaglia[2] infected pregnant guinea-pigs with trypanosomes. In one case at death the liquor amnii contained trypanosomes, in the other not; but in neither case could any parasites be found in the blood of the fetus. On the other hand, Pricolo[3] found in mice a trypanosome which was capable of traversing

[1] Pezopoulos et Cardamatis, *Centr. Bakt. und Par.*, Orig., 43, 181.

[2] *Gaz. Ospedali ed Clinichi,* 1906, 12.

[3] *Centr. Bakt. und Par.*, Orig., 43, 231.

the placenta and affecting the young *in utero*. It also appeared to multiply rapidly in the fetal circulation.

In cases of congenital syphilis, *Treponema pallidum* has been shown to be present in small numbers in the blood taken from placenta and cord and undoubtedly has the power to pass through the placental tissue from maternal to fetal circulation. While a final decision can not be reached at present, the weight of evidence favors the view that Treponema is an animal rather than a bacterium. In some closely related forms the conditions have been more definitely established. Thus in *Spirochaeta duttoni*, the cause of African relapsing fever, Breinl and Kinghorn,[4] in four rats and one guinea-pig, demonstrated the passage of the spirochete through the placenta into the fetus. The parasites were found in the placenta in approximately the same numbers as in the heart blood of the mother, yet in very meager numbers in fetal blood. There was no tendency to abort, yet a large percentage of young died shortly after birth. The spirochetes from fetal heart blood showed themselves virulent on inoculation.

These and similar cases among animal parasites are not surprising. They differ from the accidental contamination of the young at birth in the case of bacterial diseases only in that the infecting agent is capable of migration through solid tissue and thus passes barriers in the placenta which constitute obstacles to the passage not only of bacteria but also of some other animal organisms, like the plasmodium already noted, which do not penetrate tissues, but pass their entire existence in the blood stream. So far as known there is no adaptation of the parasite to special conditions and the infection of the new generation *in utero* does not differ biologically from the infection of a new organ as the parasites wander through the body of the host. The transmission of the disease to a second generation is a biological incident and bears no especial relation to the reproductive organs or function.

Certain cases are known, however, in which the conditions are radically different. One of the first of these was the demonstration by Koch[5] of the life history of *Babesia* (= *Piroplasma*) *bigeminum*. In this he was able to determine that one form in development was found in the eggs of the tick by which the organisms are transmitted. This stage appears to be the means by which the young larvæ of the second generation of ticks are

[4] Liverpool School Trop. Med., Mem. 21.

[5] *Zeit. f. Hyg.*, 54, 1.

infected. It has long been known that young produced by infected ticks will transmit certain diseases even though they have never come in contact individually with cases of the disease. The demonstration in the ova of such forms as discovered by Koch furnishes evidence of the manner of this transmission. Christophers[6] has followed carefully the formation of these bodies and their penetration into the ova, where they become spherical resting stages. He has also traced these bodies through larva to nymph and thinks that when the latter become adult the parasites have migrated into the salivary glands. It has long been known that Texas fever was conveyed by the progeny of infected ticks, but the demonstration of the infective agents has heretofore eluded observation.

Several authors, among whom Carter[7] may be mentioned, have shown that *Spirochaeta Duttoni* infects the ova of ticks which suck the blood of hosts harboring this parasite, that the organisms multiply in the ova and that by them the new generation of ticks is infected and may transmit the disease produced by the parasite. Other instances of the same type might be added to the list. The process may, however, go one step farther.

Recently reported investigations of several observers show that in the housefly a parasitic flagellate infects the ova and thus the subsequent generation of its host. Since the host is no longer a blood-sucking insect, there is no possibility of a sanguinicolous generation of the parasite in some other host. Probably the hereditary method is the only one by which the parasite is propagated and new generations of flies are infected, although it is possible that encysted forms, discharged in the feces, might be taken up in the food of some other fly. It is interesting to note in this connection some work done in my laboratory by Mr. L. D. Swingle, who has followed out the life-history of a similar flagellate parasitic in the sheep-tick. As is well known, this host is really a degenerate fly, and this parasite has, so far as can be ascertained, no relation to the blood-sucking habit of its host. It infects the ova and in a resting stage awaits there the development of the next generation, but no stages were found indicating any other method of transmission.

These instances just outlined differ radically from those noted at first in which the organisms traverse the placenta and gain entrance to the offspring *in utero*. The latter involve, as already

[6] *Indian Med. Gazette*, December, 1906, 467.
[7] *Ann. Trop. Med. and Par.*, 1, 157.

indicated, no modification or adaptation in the process of reproduction. But in the infection of the ova with a resting stage is involved a selection both of the definite organ and of the cell which becomes infected. Further, the parasite must assume a resting condition adapted to undergo successfully the changes indicated in the development of the adult insect from the eggs and sometime in the latter process must reach the suitable location. In the case of the fly such a location will be the alimentary canal of the insect, while in the tick which is to transmit the disease-producing organisms the suitable location will be rather the salivary glands, as suggested by the observations of Christophers. In any event the interrelations are evidently extremely complicated. The infection of the fetus by tissue-penetrating protozoa is purely incidental; the infection of the ova and through them of the second generation is a complicated biological process, involving essential modification in the life-history of the parasite and important morphological adaptations to new conditions of life.

A Society for the Destruction of Vermin.—Recent demonstrations as to the agency of mosquitoes, flies, bedbugs, rats and other household pests in transmitting serious diseases has taken such active hold on the British mind that there has been organized in London a Society for the Destruction of Vermin. It is incorporated under the Board of Trade regulations as a public association not formed for the object of making profit. The work the society has set itself to do is: (1) Collect information from all sources on the distribution and life-history of vermin. It will pay special attention to the part played by vermin in disease causation. (2) Disseminate as widely as possible the acquired knowledge by means of the general press, and also by special reports, leaflets and lectures. It will endeavor to make known to the public the dangers connected with each kind of vermin, the necessity for exterminating certain species, and the best means of destruction. (3) Carry out experiments in the field, test any promising measures suggested for the destruction of vermin, and, if funds permit, distribute gratuitously, to such persons as are unable to afford the expense, the necessary substances and apparatus. (4) Organize, in cooperation with other associations and public bodies, a practical campaign for the destruction of vermin. To conduct operations an active committee has been formed. (5) Encourage and assist in any legitimate

way the operations of rat and sparrow clubs and similar bodies.

The services of the society will be placed at the disposal of municipalities, boards of health, agricultural societies, shipping and deck companies, and other bodies interested in the suppression of vermin. The society has already received the support of many eminent physicians, bacteriologists and chemists, together with that of agricultural and poultry organizations, public associations and other bodies.

H. B. W.

PLANT CYTOLOGY

Polar Organization of Plant Cells.—Research in plant cytology has resulted in conflicting views as to the extent of such polar organization of plant cells as is well known for certain animals from the work of Rabl, Van Beneden, Flemming and others. Some of the algæ present clear evidence of such polarity, the best known example being Stypocaulon, which has a center in the form of an aster with a centrosome, present at the side of the resting nucleus and dividing previous to each nuclear division, or mitosis, to establish the poles of the spindle. A similar aster is present at the tetraspore mother-cells of Dictyota. Other algæ such as Fucus and Corallina show highly developed centrospheres at the poles of the spindles, but investigations so far indicate that they are formed *de novo* with each mitosis and that there are no permanent centers associated with the resting nuclei to give polarity to the cells.

The research of recent years on the cells (particularly the spore mother-cells) of pteridophytes and spermatophytes has failed to support certain claims for the presence of centrosomes in these groups of plants, and has indicated that their cells are without visible polar organization. As nuclear division approaches in the spore mother-cell fibrillæ appear in the cytoplasm, at first arranged radially, but later becoming associated in cone-shaped groups (constituting the multipolar stage), and at last arranging themselves to form the two opposite poles of the final bipolar spindle. Among the bryophytes, the liverworts have received considerable attention. In this group well-differentiated centrospheres are present at the poles of the spindles, but these are described by all investigators as arising *de novo* and they have not been reported in association with the resting nuclei.

The subject of polar organization in plant cells has received especial attention recently through the work of Harper[1] on the mildews (particularly Phyllactinia), and that of his student Marquette[2] on Isoetes and Marsilia. Harper found in the ascus of Phyllactinia an especially favorable subject for the study of the organization of the resting nucleus and its mitosis in relation to a central body, which is a permanent organ of the cell and gives to the nucleus and cell a definite polar organization. The central body lies on the nuclear membrane and the chromatin elements in an early stage of mitosis have the form of strands, each one attached independently to this center. Even in the resting nucleus, when the chromatin has the structure of a network, its attachment to the central body is evident and indicates that the strands have an individual connection with the central body as a nuclear pole. During the prophase of mitosis the central body divides and the two portions move apart to become the poles of spindle and, at the completion of mitosis, each remains connected with a daughter nucleus, thus maintaining its polarity. Furthermore, in the process of nuclear fusion within the ascus each nucleus contributes its complete polar organization so that the resulting fusion nucleus has for a time two central bodies and two independent groups of chromatic elements, which later gradually fuse into a single system with one central body.

Marquette has discovered a remarkable polarity in the leaf cells of Isoetes. Each resting cell contains a large starch-containing body, which lies so closely pressed against the side of the nucleus that the latter is usually indented. Sometimes the body is present without the starch grains that usually render it very conspicuous. Previous to nuclear division this polar structure elongates and divides by constriction and the two parts draw apart so as to form a furrow on the surface of the nucleus. The separated halves then come to lie at opposite ends of the nucleus, which has become somewhat elongated. These developments take place before the appearance of the chromatin gives

[1] Harper, R. A. Sexual Reproduction and the Organization of the Nucleus in Certain Mildews. *Pub. Car. Inst.*, No. 37, 1905.

[2] Marquette, W. Manifestations of Polarity in Plant Cells which Apparently are without Centrosomes. *Beih. Bot. Centralbl.*, XXI, p. 281, 1907. Concerning the Organization of the Spore Mother-cells of *Marsilia quadrifolia*. *Trans. Wis. Acad. Sci. Art. Let.*, XVI, p. 81, 1908.

indication of the approaching mitosis. As the prophases of mitosis become evident the two polar structures move away from the nuclear membrane, become much flattened, and spindle fibers develop in the region between the two. The polar structures then round up so that in the metaphase of mitosis they are irregularly rounded bodies at the poles of the spindle against which the ends of the spindle fibers press. During anaphase the chromatin of the daughter nuclei comes to lie closely against the surface of the rounded polar structures, and each daughter nucleus when fully formed is deeply indented or kidney-shaped in sections. The amount of starch decreases during the prophases, indicating that there is a consumption of starch at the time of the mitosis. The polar structures increase in size during telophase and remain at the side of the daughter nuclei until the above history is repeated with the next mitosis.

In the spore mother-cells of Marsilia, Marquette has found evidence of polar organization at the time of synapsis. Following the differentiation of the spore mother-cells there is a period of growth during which starch grains appear, first in a scattered arrangement, but soon in a specified region between the nucleus and the wall of the spore case, a situation favorable for an interchange of metabolic movements between the nucleus and the surrounding tapetum. There is thus a polarity of the cell, which presently becomes more conspicuous by the changes characteristic of synapsis within the nucleus. The chromatic material during synapsis converges to a point on the nuclear membrane against which lies a nucleole, and the entire mass of contracted chromatin is directly opposite the assemblage of starch grains in the cytoplasm adjacent to the nucleus. The nucleus, then, during synapsis presents a definite polar side with its chromatin content contracted at a point opposite the assemblage of starch grains, and an antipolar side free from chromatic substance, where also the nuclear membrane appears much heavier than in the region of the synaptic mass.

Fibers become conspicuous in the cytoplasm during synapsis, especially on the antipolar side of the nucleus, and these tend to become arranged in cone-shaped groups as the nucleus passes out of synapsis. There is at times a bipolar arrangement of the fibers, but later several well-defined poles are developed and a multipolar stage results which is similar to the multipolar spindle characteristic of spore mother-cells. The cones of the

multipolar spindle finally become grouped to form a typical broad-poled bipolar spindle. During the mitosis the starch mass lies at the side of the spindle, but as telophase comes on, it gradually moves in between the two daughter nuclei, forming an irregular thin plate between the two. This starch plate separates the two spindles of the second mitosis which lie at various angles to one another. After the four granddaughter nuclei are formed the starch becomes distributed in about equal amounts to the four cells. The polar organization of the spore mother-cell of Marsilia, conspicuous at the time of synapsis, then disappears, according to Marquette, just before the formation of the first spindle. Marquette, however, seems inclined to believe that more careful study of multipolar stages in spindle formation may establish a continuous polar organization throughout these mitoses.

These investigations of Harper and Marquette are likely to stimulate further research upon the polarity of the plant cell, and a more critical reinvestigation of favorable types where an isotropic or radial structure is believed to obtain. It may, nevertheless, be found that polarity will not depend in all cases upon the presence of permanent protoplasmic structures of sufficient size or morphological differentiation to rank as organs of the cell. There may be polarity at times without visible protoplasmic organization. It is probably very unusual for a cell to be so situated that its activities are expressed in a strictly radial fashion; there is rather certain to be an upper or lower, an inner or outer, or a one-sided relation to important environmental conditions, and these may be expected to develop metabolic centers, which, at times, may in their turn create such protoplasmic differentiation along an axis as to establish an evident polar organization of the protoplasm.

Further evidence of polar organization in plant cells is presented in the structure and development of the cilia forming organs, or blepharoplasts. Some recent research on these structures will shortly be reviewed in the Naturalist.

Bradley M. Davis.

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PROFESSOR S. A. FORBES

University of Illinois

In the course of a statistical survey of the bird population of the State of Illinois, begun with a view to a better knowledge of the significance of birds in the economy of nature, two field observers, A. O. Gross and H. A. Ray, engaged in this work as assistants on the State Natural History Survey, spent virtually a month of the summer period of 1907 in each of the three principal sections of the state—June in southern, July in central, and August in northern, Illinois. Selecting in each section a locality typical for that part of the state, they made regular trips on foot in various directions and to various distances, traveling always thirty yards apart, and noting as they went the species and numbers of all birds flushed by them on a strip fifty yards in width, including likewise those flying across this strip within a hundred yards to their front. They kept record, also, by means of mechanical counters, of the distances traveled over each distinguishable kind of area, commonly marked by the crop which is borne.

The present paper is a report of a few of the more general results of a study of the materials thus brought together, illustrating the numbers and ecological distribu-

[1] Read before the Central Branch of the American Society of Zoologists, Chicago, January 2, 1908.

tion of the birds of Illinois during the relatively stable period of their summer residence—the time between the conclusion of the spring migration and the beginning of the fall movement to the southward. It is a period of breeding and steady habitation for our most permanent and characteristic bird population, and will best help us to an understanding of the main normal ecological significance of Illinois birds.

The Area of Observation

The total distance traveled by my observers on these various mid-summer trips was 428 miles (omitting fractions), of which 141 miles was in southern Illinois, 112 in central, and 175 in northern. The total area covered by this strict census of the bird population was a trifle over 12 square miles, or 7,693.5 acres—33 per cent. of this acreage being in the southern, 26 per cent. in the central, and 41 per cent. in the northern, part of the state—or approximately a third of this area in southern, a fourth in central, and two fifths in northern, Illinois. The field observations began in the south June 4, and ended at the north August 23, with the idea of avoiding, so far as possible, by this order of progress, differences due to different seasonal conditions. It was not possible, of course, to eliminate these wholly, with only one pair of observers; and it will tax our ingenuity, and sometimes perhaps overtax it, to detect these differences and to distinguish them from those due to mere difference of latitude and of climate corresponding.

The total surface on which these precise mid-summer observations were made was 1/4,720 part of the whole state, and the question at once arises, Was this area sufficient to give these results any general value for the state at large, and, if so, how may we be sure of it? There is, I believe, no mathematical method of determining the sufficiency of these data for generalization purposes, and I know of no test at present applicable except that of the general consistency and reasonableness of the totals,

averages and ratios, for the different districts and seasons, the presence or absence of which each can readily see for himself as this discussion proceeds. If the data of observation are insufficient for the uses made of them, there will be a random variability and inexplicable irregularity in my statistical summaries which we shall not fail to notice.

General Product of the Survey

Gross and Ray identified during the summer, on the territory covered by their data, 7,740 birds, belonging to 85 species. This is at the rate of 645 birds per square mile, or almost precisely 1 per acre, including the so-called English sparrow. If we omit the 1,414 interloping English sparrows observed—which is a little more than 18 per cent. of the entire number of birds—we have remaining 527 *native* birds to the square mile. The total for Illinois,[2] on this basis, is 30,750,000 native birds and 5,536,000 English sparrows, or approximately 14 summer resident birds to each person in this state living in the country or in towns of less than 25,000 inhabitants.

Of the 85 species represented by the 7,740 birds recognized on these trips, the 21 most abundant species were represented by 6,596 birds. That is to say, 85 per cent. of the birds belonged to 25 per cent. of the species. The 21 more abundant species numbered, taken together, 550 to the square mile, and the 64 less abundant species, taken together, numbered 95 birds to the square mile, or 1 to every 6¾ acres. The latter species are evidently negligible as general factors in the ecological system, and attention need be given, in discussing the birds of the state as a whole, only to the 21 species common enough to produce some appreciable general effect. Given in the order of their abundance they are as follows:

[2] A combination of the averages for the three sections of the state, computed separately, the data for the sections being differently weighted to compensate for differences in area.

A. O. U. Nos.	Bird	No. Observed	Per Cent.
X	English sparrow	1,414	18.4
501	Meadow-lark	1,025	13.2
511b	Bronzed grackle	900	11.6
316	Mourning-dove	461	6.
604	Dickcissel	393	5.1
498	Red-winged blackbird	347	4.4
474b	Prairie horned lark	296	3.8
412	Flicker	197	2.6
761	Robin	194	2.5
563	Field-sparrow	186	2.4
529	American goldfinch	158	2.
444	Kingbird	126	1.8
494	Bobolink	119	1.5
546	Grasshopper sparrow	110	1.4
705	Brown thrasher	104	1.3
495	Cowbird	102	1.3
406	Red-headed woodpecker	99	1.3
613	Barn-swallow	96	1.2
289	Quail	91	1.2
261	Bartramian sandpiper	89	1.1
488	Crow	89	1.1
		6,596	85.2

Variation with Latitude

The English sparrow decreases in abundance from north to south, from 147 to the square mile in northern to 113 in central, and 82 in southern, Illinois. One hundred sparrows in the northern part of the state are thus represented by 77 in the central and 56 in the southern part.[3] The *native* summer residents, on the other hand, increase in numbers from north to south, the birds per square mile being 464, 537 and 600 for nothern, central and southern Illinois, respectively. That is, 100 native birds in northern Illinois were represented in mid-summer by 116 in central and 129 in southern Illinois. The decrease in English sparrows from north to south is not sufficient to offset the increase in the native species, the total numbers per square mile for all summer birds in the three sections of the state being 610, 650 and 682—or 100 birds in northern for 107 in central and 112 in southern Illinois.

This same gradation was much more pronounced in the record of the *winter* residents. From the last of Novem-

[3] Since the above was written, my attention has been called, by Dr. Hans Gadow, to the fact that in Europe also this sparrow diminishes in number southward.

ber to March 15, birds averaged 384 to the square mile in northern Illinois; from December 23 to March 21, 582 to the mile in central Illinois; and from February 6 to February 21, 832 to the mile in southern Illinois, numbers related to each other as 100, 151 and 217. Indeed, we find birds more abundant in extreme southern Illinois in the mid-winter period of 1906–07 than in the mid-summer period of 1907, averaging at the rate of 122 birds in the former season to each hundred in the latter.

If we take into account the numbers for the whole year, there are, for every hundred birds in the northern part of the state, 133 for central and 181 for southern Illinois.

BIRDS BY SECTIONS

	Northern Illinois	Central Illinois	Southern Illinois
Summer:			
Native	100	116	129
Sparrows	100	77	56
All birds	100	107	112
Winter:			
Native	100	170	292
Sparrows	100	65	1
All birds	100	151	217
Whole year:			
All birds	100	133	181

The bobolink was a distinctively northern bird, occurring in the ratio of 24 to the square mile in northern Illinois, and not at all in either of the other sections. The mocking-bird, on the other hand, was almost exclusively southern, being represented by 8 birds to the square mile in the southern section, by only 1 specimen seen in central Illinois, and not at all in the northern part of the state.

MIGRATION WAVES

In a paper published last April under the title "An Ornithological Cross-section of Illinois in Autumn," [4] I gave the data and results of a trip across central Illinois made by Gross and Ray during the fall of 1906. A comparison of the general average of the bird population,

[4] Bull. Ill. State Lab. Nat. Hist., Vol. VII, art. 9.

determined from the data of this trip for the period of the fall migrations, with the mid-summer average for the same section of the state, as determined last July, shows an interesting difference which leads us to consider the effect of the autumnal movement to the south on the numbers of the local bird population. On the above trip across the state, made between August 28 and October 17, 1906, a general average of 579 native birds to the square mile was found, while the corresponding mid-summer average for the present year is 537 native birds to the square mile—a difference of 42 birds to the mile, or nearly 8 per cent., in favor of the fall population.

Native Birds per Square Mile, Fall (1906), Summer (1907)

	Migrant	Resident	Total
Summer		537	537
Fall	98	481	579
Difference	+98	—56	+42

Was this difference due to the fact that the fall migration was in progress when last year's observations were made? That is, does the migration movement begin first at the north and result in a local wave of increased numbers, birds coming in from the north earlier and faster than the resident species leave for the south? It is possible to answer this question by reference to the data of the paper just cited.

An analysis of the list of species identified on last year's autumnal trip shows that 481 per square mile of these birds were summer residents, still remaining, and that 98 per square mile belonged to migrant species, on their way to the south. The summer residents still present in this autumnal period were thus 56 per square mile fewer than the resident birds of the present summer. That is, 56 summer residents for each square mile of central Illinois had gone south, on an average, and 98 fall migrants had, on the other hand, come in to take their place, the difference between these numbers giving us

the excess of 42 birds per square mile of fall over summer. This temporary increase of 8 per cent. in autumn in the average number of our birds is thus evidence of a wave of condensation running southward in consequence of the earlier beginning and more rapid development at the north of the annual fall migration.

This contrast of the number of the resident summer population with that of the fall migration period is still more clearly and strongly shown by a comparison of the totals of all our central Illinois observations in mid-summer and in fall, respectively. These average 1.07 birds to the acre for the period from July 9 to September 21, and 2.31 per acre for the interval between the 1st and the 26th of October. That is, more than twice as many birds per acre were seen in October of this year as in July, August and September.

The data of the *spring* migration of 1907 are unsatisfactory owing to the extraordinary character of the season, and the consequent repeated interruption and remarkable prolongation of the movement. Nevertheless, they indicate a larger population during the early part, at least, of this migration period also than either before or after it. A trip down the eastern side of the state from Cook to White county, begun March 26 and ending April 11, gave an average of 1.34 birds to the acre—a number to be compared with our mid-summer average for the whole state, which is 1.03. That is, the average early spring population of this exceptional year was 30 per cent. greater than the average of the summer following. On the other hand, a trip across central Illinois between April 20 and May 29, still within the migration period, gave us, for 5 1/3 square miles of area, an average of only .89 per acre—less than even the mid-winter average of .91 for the same part of the state.

Vegetation of the Inspection Area

As a basis for a more precise account of the distribution of birds as a whole and of the more important

species, it will be necessary to consider the vegetable covering of the soil, since there is little else in Illinois by which different portions of its area may be distinguished. The territory traversed by my observers, it need hardly be said, was almost wholly under cultivation. Excluding only forests in which the trees were too high, or the undergrowth was too dense, to permit a full and accurate census of the birds, the territory reported upon was chosen wholly at random, and the total for each division of the state seems sufficient to give us, with the exception just mentioned, a fair sample of its crops and surface conditions. The areas from which all the birds were determined were 3,172 acres for northern Illinois, 2,117 acres for central, and 2,504 acres for southern.

In the upper third of the state, 95 per cent. of the surface was in corn, small grain and grass—31 per cent. in corn, 27 per cent. in small grain (nearly all of it oats) and 37 per cent. in the pasture and meadow crops, about equally in each. In the central region the area in corn rises to 46 per cent. of the whole, that in small grains was about 26 per cent. (again nearly all oats) and that in the forage crops was 27 per cent. (the pasture lands nearly twice as extensive as the meadows)—a total of 99 per cent. of the area examined which was devoted to these great farm crops. In the lower third of Illinois only 23 per cent. of the land was in corn, an almost equal area (21 per cent.) was in small grain—more than half of it wheat—and 44 per cent. was in grass, clover and similar forage plants, rather equally divided between pastures and meadows. That is to say, the areas in corn and small grains were nearly the same, and these together were barely equal to the meadows and pastures. The

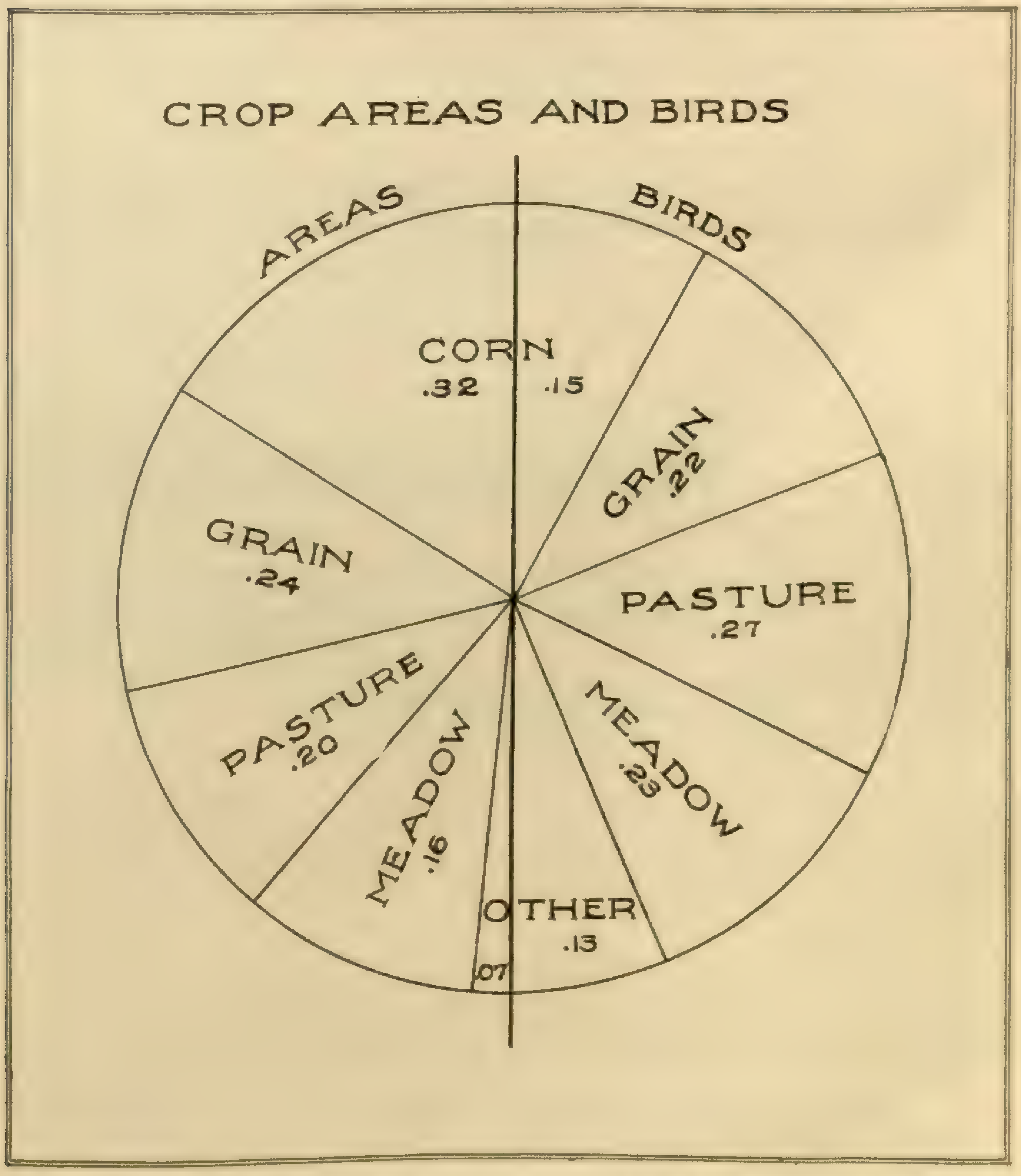
Crop Areas. Per Cent., 1907

	Northern Illinois	Central Illinois	Southern Illinois
Corn	31	46	23
Grain	27	26	21
Grass	37	27	44
Miscellaneous	5	1	12

total in all these crops was 88 per cent. of the area inspected, the remaining 12 per cent. covering the orchards, the more open woods, the waste and untilled lands, and a few additional minor items.

NUMBERS OF BIRDS BY CROPS

Illinois is still a prairie state in the predominance of birds which prefer a grassy turf as an abiding place.



Almost exactly half of those recorded for the state last summer were from pastures and meadows, although the

total acreage in these lands was but 36 per cent. of the entire area inspected. These figures are equivalent to a density ratio on pastures and meadows of 1.39 for all the birds of the state.[5] Corn is an exotic crop in Illinois, and birds were only about a third as abundant in corn fields as in grass lands, while in small grains they were nearly twice as abundant as in corn. The acreage in these crops was such that 15 per cent. of all the birds of the season were found in corn fields and 22 per cent. were in small grain. In orchards they averaged 4½ times as numerous to the unit of area as in fields of grain, 2,471 to the square mile—giving a density ratio of 3.84; but the acreage in orchards from which the birds were identified was so small that all the orchard birds together amount to only 2 per cent. of the whole number observed. Among native trees and shrubbery, birds were much less abundant than among fruit trees, and the density ratio for these situations was about 2.25.

By way of further illustration of the application of this quantitative method to the subject of local distribution, I will present some of the more pronounced results for one species of bird throughout its range in summer, and for one kind of crop area as visited or inhabited by midsummer birds.

THE MEADOW-LARK

One thousand and twenty-five meadow-larks were identified by my observers in their work on the summer residents of the state, an average of 85 to the square mile for the whole area traversed by them. As these birds were unequally distributed, never occurring, for example, in woodlands or among shrubbery, their numbers rose in some situations far above this general average, amounting to 266 to the square mile in stubble, 205 in meadows, 160 on untilled lands, 143.5 in pastures, and 131 on waste lands, and falling to 10 to the square mile in fields of corn.

[5] That is, taking an average density of the bird population for the whole area of the state as 1, the density in pastures and meadows only is 1.39.

MEADOW-LARKS PER SQUARE MILE. SUMMER, 1907

Stubble	266
Meadows	205
Fallow	160
Pastures	143.5
Waste	131
Corn	10
Woods	—
Shrubs	—
State	85

They varied also in abundance, in a very interesting way, from the north to the south. One hundred of them in northern Illinois were represented by 175 in central and by 215 in southern Illinois. This variation was evidently independent of any difference in the extent of surface covered by the kinds of vegetation which they most prefer, since the ratio of pasture, meadow, waste and untilled lands taken together was considerably less for central than for northern Illinois, although the meadow-larks were 75 per cent. more numerous; and it was only a fourth greater for southern Illinois than for northern, although the meadow-larks were more than twice as abundant. The cause of the greater numbers southward, so far as I can see, can be accounted for only rather vaguely as climatic.

Much more difficult of even general or hypothetical explanation is a curious difference in the observed abundance of meadow-larks in pastures and meadows respectively, in the three divisions of the state. In northern Illinois there were 87 larks per square mile in pastures to 129 in meadows; in southern Illinois there were 125 in pastures to 297 in meadows; while in central Illinois this relation was reversed, the number in pastures being 274 to the mile, and that in meadows 189. That is, while 100 pasture birds were represented in northern Illinois by 148 in meadows, and in southern Illinois by 242, in central Illinois they were represented by only 69. Since the southern Illinois observations were made in June, those for central Illinois in July and those for northern

Illinois in August, one naturally looks to differences in season, in the advancement of the crops, or in agricultural operations as related to the haunts and habits of these birds, for an explanation of their apparent shift from meadows to pastures in July in central Illinois, and a seemingly plausible explanation is suggested by the fact that haying was mainly done during July in the central part of the state, but was not yet fairly begun in southern Illinois in June and was nearly over in northern Illinois in August.

Pasture Birds per Square Mile. Summer, 1907

Meadow-larks

	Northern Illinois	Central Illinois	Southern Illinois
Pasture	87	274	125
Meadow	129	189	297

Other Pasture Birds

	Northern Illinois	Central Illinois	Southern Illinois
Pasture	50	54	120
Meadow	200	131	371

If, however, the meadow-larks were disturbed to this extent by the operations of making and saving the hay crop, one would expect to find the other distinctively meadow birds similarly affected—a supposition which is not borne out by the facts of our record. Besides the meadow-larks, there were five common species more abundant in meadows in one or another section of the state than in any other important situation; namely, the red-winged blackbird, the purple grackle, the vesper-sparrow, the grasshopper sparrow, and the dickcissel. Each of these species was, moreover, more abundant in meadows than in pastures in each section of the state—in central Illinois as well as in the other two—excepting only the grackle in southern Illinois. Taking all five of these birds together, there were in northern Illinois 200 to the square mile in meadows and 50 in pastures, in central Illinois 131 and 54, respectively, and in southern Illinois 371 and 120. In other words, for each hundred of these

five kinds of birds in meadows, there were, in the northern section, 25 of them in pastures, in the central section 41, and in the southern section 32. The cause of this apparent change in the preference of the meadow-larks of central Illinois seems, therefore, something peculiar to themselves, and is still to seek.

Birds of the Pastures

The birds of a given situation may be discussed from two quite different standpoints, both interesting and pertinent, and both really necessary to a complete understanding of the facts. We may consider the members of an assemblage of species there with first reference to their relative importance to the situation itself—with reference, that is, to their comparative numbers, or to the nature and effect of their activities; or we may consider the situation with first reference to its relative importance in the economy and life of each species of bird which inhabits or visits it. If this situation is woodland, for example, a bird found only in forests might, if a comparatively rare species, have very little importance—might produce very little effect in the situation because of its infrequent occurrence there, while to the species itself the forest situation would be all-important, as the sole place of its habitation. Its own significance in forests might be easily overbalanced by a very abundant species which should visit woodlands only occasionally, but whose average numbers there might be twice or thrice as large to the unit of area and time as those of the less abundant species inhabiting forests exclusively. Time will not permit me to illustrate this division of my topic from both these points of view, and I will limit myself to a few words in conclusion on the *pasture birds* as a group and on some of the more prominent pasture species with reference to their importance in pastures.

Pasture lands were the preferred resort of our most abundant mid-summer birds. That is, more birds were seen in pastures than in any other of the larger crop areas

of the state—2,107 in that situation as against 1,814 in meadows, 1,667 in fields of small grain, and 1,169 in fields of corn. Indeed, 27.2 per cent. of all the mid-summer birds determined by my observers were seen in pastures, 23.4 per cent. in meadows, 21.5 per cent. in small grain, and 15.1 per cent. in corn. The area in pastures was larger than that in meadows, however, and on this account, if we consider the number of birds per square mile, we must change this order of precedence. With a general mid-summer average of 645 birds to the square mile for the whole state, we have 920 to the mile for meadows, 878 for pastures, 962 for small grain, and 300 for corn. Or, if we take the number per square mile for the entire state as 1, 1.43 will be the density ratio for meadows, 1.36 for pastures, .87 for grain fields, and .47 for corn fields.

SUMMER BIRDS IN CROPS, 1907

	Numbers	Ratio	Per Square Mile	Densities
Pastures	2,107	27.2	878	1.43
Meadows	1,814	23.4	920	1.36
Grain	1,667	21.5	562	.87
Corn	1,169	15.1	300	.47
Other	983	12.8		

Looking to the composition in species of this mid-summer pasture population, we find that more than half the summer resident birds of Illinois pastures belong to five species—the English sparrow, the meadow-lark, the crow-blackbird, the horned lark and the field-sparrow, relatively abundant in the order named; and this statement is almost as true of the three sections of the state as it is of the state as a whole. Comprising nearly 53 per cent. of the pasture birds of the entire state, these five species made 49 per cent. of those of northern Illinois, 61 per cent. of those of central Illinois, and 47.5 per cent. of those of southern Illinois. Indeed, the first four of these species were the most abundant pasture birds of the whole state for the whole year, occurring there in the following numbers: English sparrow, 1,394; crow-blackbird, 696; meadow-lark, 686; horned lark, 603; and field-sparrow,

230. These are consequently our most typical pasture birds. In the pastures of the state at large the English sparrow was the most abundant species, making 20 per cent. of all the birds seen in pastures during the summer months, and the meadow-lark was nearly as common, making 17 per cent. of these birds. The meadow-lark was, indeed, the *most* abundant pasture bird in both southern and central Illinois, the sparrow surpassing it only in the northern division of the state. The horned lark, on the other hand, was second in northern Illinois, but tenth in both central and southern Illinois, and fourth for the state as a whole. The crow-blackbird was third on the list for the whole state, fourth for southern Illinois, third for central, and sixth for northern Illinois.

Ten species comprised more than two thirds of the pasture birds of the state, and these same ten species made 63 per cent. of the birds of northern Illinois pastures, 80 per cent. of those of central Illinois, and 64 per cent. of those of southern Illinois. Besides the five species already mentioned, these were the flicker, the robin, the mourning-dove, the red-headed woodpecker, and the red-winged blackbird.

One general impression made by this preliminary examination of the present bird population of the State of Illinois is that of a remarkable flexibility and tenacity of the associate and ecological relationships of birds in the face of revolutionary changes in their environment. Apart from the results of the introduction of the English sparrow, and the direct destruction of game birds and birds of prey, the main effect of human occupation seems to have been the withdrawal of most of the prairie birds from the area devoted to Indian corn, and their concentration in pastures, meadows, and fields of small grain—situations which most nearly resemble their original habitat.

THE LIFE CYCLE OF PARAMECIUM WHEN SUBJECTED TO A VARIED ENVIRONMENT

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STUDIES on the life cycle of *Paramecium aurelia* (*caudatum*) have been made by several investigators, the most extensive work being that of Calkins.[1] As is well known, his results showed that when Paramecium was bred continually in a culture medium of hay infusion, it passed through more or less regular cyclical variations in general vitality as measured by the division-rate. The marked periodical depression periods occurred at about six-month intervals and unless the organisms were "stimulated" at this time the culture died out. Minor depressions occurred about every three months, but from these recovery was autonomous. Joukowsky[2] and Simpson,[3] however, apparently found that certain cultures of this organism died out after being but a short time under culture conditions.

A constant culture medium is an important condition for the study of the consecutive phases of vitality, and of the effect of stimuli on the organism, but it is of interest, however, in the light of the results obtained by this method to determine the character of the life cycle of Paramecium when subjected to a varied environment. It is possible, of course, that some element is lacking in

[1] Calkins, G. N. Studies on the Life History of Protozoa. I, The Life Cycle of *Paramecium caudatum*. *Archiv f. Entwk.*, XV, 1, 1902. IV, Death of the A Series. *Journal Exper. Zool.*, I, 3, 1904.

[2] Joukowsky, D. Beiträge zur Frage nach den Bedingungen der Vermehrung und des Eintrittes der Konjugation bei den Ciliaten. *Verh. Nat. Med. Ver. Heidelberg*, XXVI, 1898.

[3] Simpson, J. Y. Observations on Binary Fission in the Life History of Ciliata. *Proc. Royal Society Edinb.*, XXIII, 1901.

a constant culture medium of hay infusion which is essential to the continued life of the organism, and that depression effects which appear more or less regularly are due, in part, to a process of slow starvation—rather than to a loss of the power of assimilation. Recovery from these periods is effected by various stimuli (beef extract, etc.), because the lacking factor, or factors, is thereby supplied. Calkins himself points out the marked similarity of the morphological changes which he obtained in the earlier cycles of his Paramecium cultures with those found by Wallengren[4] to occur in Paramecia which had been intentionally starved. I have also called attention to this similarity in discussing the life cycle of various hypotrichous infusoria and have suggested that the effect of such stimuli as beef extract, etc., may be essentially that of concentrated nutrition.[5]

In connection with some experiments on the effect of various stimuli on the life cycle of infusoria,[6] I have had occasion to carry a culture of Paramecium for over a year, and the data derived from this work are believed to throw some light on the effect of a varied environment on the life history of this organism.

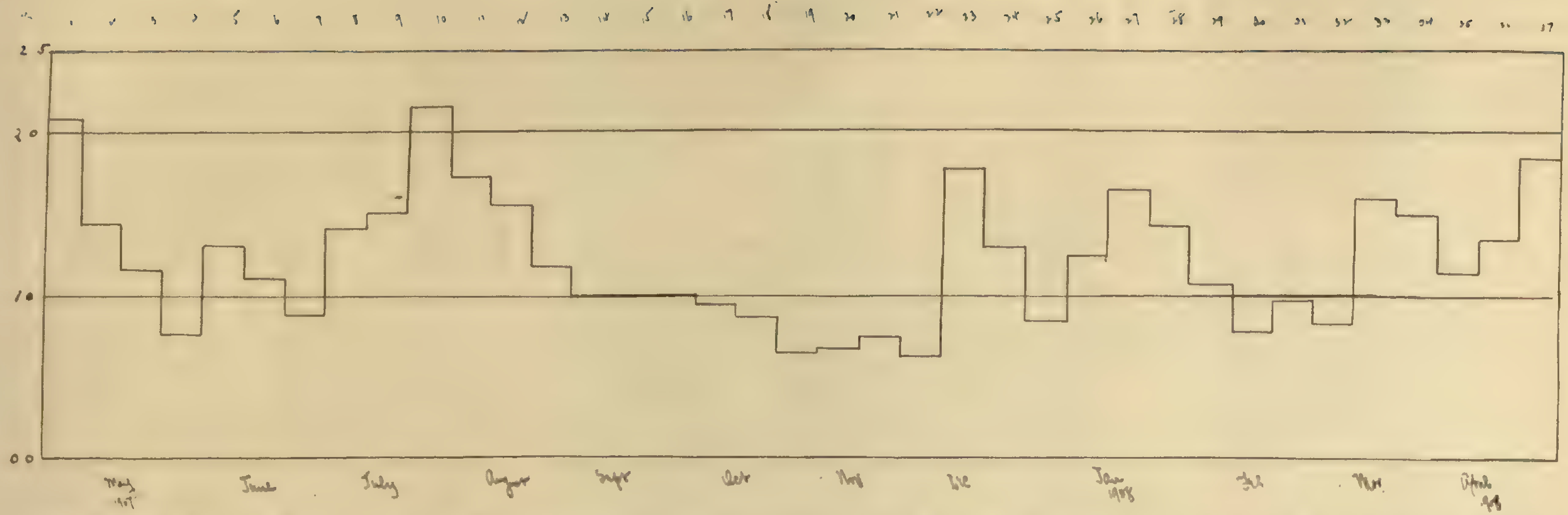
On May 1, 1907, a "wild" Paramecium was isolated from a laboratory aquarium and placed on a depression slide in five drops of hay infusion. When this animal had divided twice, the four resulting individuals were isolated on separate slides, and in this manner were started the four lines, I-a, I-b, I-c and I-d, which compose this culture.[7] The culture has been continued by the isolation of an individual from each of these lines almost daily throughout the life of the culture up to the present time (May 6, 1908) and a record has been kept of the

[4] Wallengren, H. Inanitionserscheinungen der Zelle. *Zeit. f. allg. Physiologie*, I, 1, 1901.

[5] Woodruff, L. L. An Experimental Study on the Life History of Hypotrichous Infusoria. *Journal Exper. Zool.*, II, 4, 1905.

[6] Woodruff, L. L. Effects of Alcohol on the Life Cycle of Infusoria. *Biol. Bull.*, XV, 2, 1908.

[7] Further details in regard to the technique are given in previous papers.



Complete history of *Paramecium aurelia* (*caudatum*). Culture I, from start on May 1, 1907, to the present time, May 6, 1908, at the 465th generation. The rate of division is averaged for ten-day periods. The ordinates represent the average daily rate of division of the four lines of the culture. Above, the numbers of the ten-day periods are indicated. Below are designated the periods in which the fifteenth day of the respective months fell. The figures, 100, 200, etc., represent generations and are placed in the periods in which they were attained.

daily bipartitions of each line. The following curve represents graphically the average rate of division of the four lines of the culture, and this again averaged for ten-day periods.

The culture was carried on at the Thompson Biological Laboratory of Williams College, Williamstown, Mass., during May and June, 1907; at the Marine Biological Laboratory, Woods Holl, Mass., during July and August, 1907; and at the Sheffield Biological Laboratory of Yale University, New Haven, Conn., from September, 1907, to the present time, May, 1908.

The culture medium during the earlier months of the work consisted of hay or grass infusion. But, except during periods in which the culture was employed as a control for certain experiments, the infusion was made with hay or grass from various localities and different proportions of hay and water were used almost daily. Water from various sources was employed. In every case the temperature of the infusion was raised to the boiling point, and then allowed to attain the temperature of the laboratory before being used. In some cases the infusion was made fresh daily, in other cases it was allowed to stand twenty-four hours before being used.

Beginning in February, 1908, a much more varied culture medium was employed. It was found that Paramecium can exist in nearly any infusion which may be made from materials collected in ponds and swamps, and accordingly, in the hope of supplying as far as possible all the elements which may be encountered in the "normal" habitat of the organism, water was taken from ponds, laboratory aquaria, etc., together with its animal and plant life. In other words, no definite method was employed in selecting the material, but it was simply collected at random from many sources, thoroughly boiled, and then used. This culture medium affords a striking contrast to that employed by Calkins, which he described thus, "The hay infusion was made every day, the same amount of hay and water being taken each time and

raised to the boiling point. This method was never varied during the entire period of the cultures and the salt content of the water, as shown by weekly analyses, did not vary beyond a very slight fraction of one part to one hundred thousand."

The only condition present in the life of this culture which could not be encountered by a wild Paramecium was the boiled condition of the culture medium, but this was essential in the experiments in order to prevent the introduction of an encysted or active wild individual into the culture.

The objection might be made that the environment was changed too frequently and too greatly to afford natural conditions. But, if the hundreds of millions of wild individuals which are derived from a single wild Paramecium are considered, and if the environment of any four lines of descent of four individuals existing at the end of twelve months in the wild state is taken into account, it will be readily appreciated that the surviving organisms have probably experienced far more changes of medium than have the four lines of the culture under consideration. It may be that only those individuals which have encountered varied conditions have survived without resorting to conjugation.

It is obvious, indeed, that all the variations in environment which may be experienced by a wild Paramecium have not been supplied; for in a pond considerable changes of temperature occur during the year, and periods of rest by encystment or lack of food are afforded. It is believed, however, that the conditions under which this culture has been carried approach nearer to those encountered by the majority of wild individuals than has been the case in previous investigations.

A glance at the plotted curve of the life history shows that at no ten-day period during the life of the culture up to the present time has the average rate of division of the culture fallen as low as one division in two days, the nearest approach to this rate being attained at period

twenty-two in December, 1907, when the culture was subjected to a particularly uniform culture medium. The highest rate of division so far attained occurred at period ten in July, 1907. The average rate of division for the entire year is obviously considerably above one division per day, the organisms being in the 465th generation on May 6, 1908. That this is not the maximum rate of division of which the culture is capable is shown by the fact that a culture isolated line by line from the one under consideration and treated daily for six months with alcohol is at the same date in the 505th generation.

The major fluctuations in the division rate which have occurred in the life of this culture are all "rhythms" (using this term in the sense in which I employed it in discussing the life history of Oxytricha) and so far no "cycle" has been completed. Calkins in his earlier papers on Paramecium believed the cycle to be of three months' duration, agreeing in this regard with certain of the earlier investigators on this form. In his last paper on the subject, however, as has been noted, he interpreted the tri-monthly fluctuations as simply minor changes from which recovery was autonomous and regarded the cycle as the larger semi-annual fluctuations, recovery from which was only brought about by stimuli. I have previously interpreted these trimonthly depressions as rhythms and the results obtained from this culture would seem to show that the semi-annual cycles of Calkins are also merely rhythms—recovery from which was not autonomous under the conditions of a constant environment. This culture shows that the cycle of Paramecium under a varied environment may be considerably over a year in duration, since the culture at present shows no sign of waning vitality.

This suggests the much-discussed question as to whether the protozoa are potentially immortal, and the rôle of conjugation in the life history. Up to the present time there has been no tendency among the individuals of this culture to conjugate, although in the "stock" cultures,

comprising individuals left over after the daily isolations, there has been every opportunity for its occurrence. Of course there has been no possibility of conjugation in the four direct lines of the culture on account of the daily isolations. This result agrees with that which I obtained with my cultures of various hypotrichous forms—and I believe it suggests strongly that conjugation must be regarded as a more or less variable phenomenon which occurs in the life history when conditions are adverse for the normal life of the organism, and which is not necessary under the conditions of a varied environment. I believe it is customary to regard conjugation as of far more frequent occurrence than it actually is in the life history of "wild" individuals, because it is brought to the attention in laboratory cultures and "hay infusions" which pass through a series of changes—changes which inevitably bring about conditions unfavorable to the continued reproduction of the organisms, and which are compensated for by conjugation.

No period of marked physiological depression is indicated by the division-rate of this culture during the first year of its life; but well-defined morphological changes have occurred. These cytological variations, chiefly nuclear, demand further study. It is evident, however, that the relation of the rate of division to the so-called "normal" condition of the nuclear apparatus of Paramecium is not substantiated by this culture, as profound nuclear changes apparently do not affect the rate of division. I believe from a study of this culture and "wild" cultures in large laboratory aquaria, that various nuclear changes which are not at present recognized occur normally in the life history of Paramecium, and that possibly when conjugation between two individuals is prevented, either under the conditions of culture or in the "wild" state, a rearrangement of the nuclear apparatus is resorted to which may be analogous to endogamy, or conjugation of nuclei within the original cell.

PLACOBDELLA PEDICULATA n. sp.[1]

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In the summer of 1889, while at Lake Pepin superintending the zoological work of the Geological and Natural History Survey of Minnesota, Professor Nachtrieb found that some of the sheepsheads (*Aplodinotus grunniens*) which were being seined from the lake in large numbers by the local fishermen had a large parasitic leech fastened to the isthmus or shoulder under the gill cover. Three of these leeches were collected at that time, with portions of the fish showing the place and manner of attachment. One of these specimens was later sent to Professor J. Percy Moore, who found it to be a new species of *Placobdella* and suggested the specific name *pediculata*. All the specimens originally collected were adults, gorged with blood, and greatly modified in form from the usual *Placobdella* types by their close parasitic habit; so that, in some parts, annulation and many other external features had been entirely obliterated. It was seen at once that to determine these features younger and better-preserved specimens must be obtained. Accordingly, during the first part of September, 1903, I spent several days with the fishermen around the head of Lake Pepin examining fish for this leech. During this time I examined many hundreds of fish and succeeded in obtaining three small specimens, none of which were over a centimeter in length.

HABITS

Placobdella pediculata appears to be a true fish parasite, having been found only in the gill chamber of the

[1] From the laboratory of the Department of Animal Biology, the University of Minnesota.

fresh-water sheepshead, the posterior sucker of the leech being deeply imbedded in the side of the isthmus or shoulder. In the case of young leeches which have not been long attached, the depression caused by the posterior sucker is comparatively shallow, being a mere external depression in the inflamed tissues of the fish. As the attachment continues the inflamed tissues of the host grow up like a collar and close in around the leeches body in front of the sucker. This closing in of the inflamed collar presses upon the body of the leech, narrows it to a slender peduncle in front of the sucker and in-

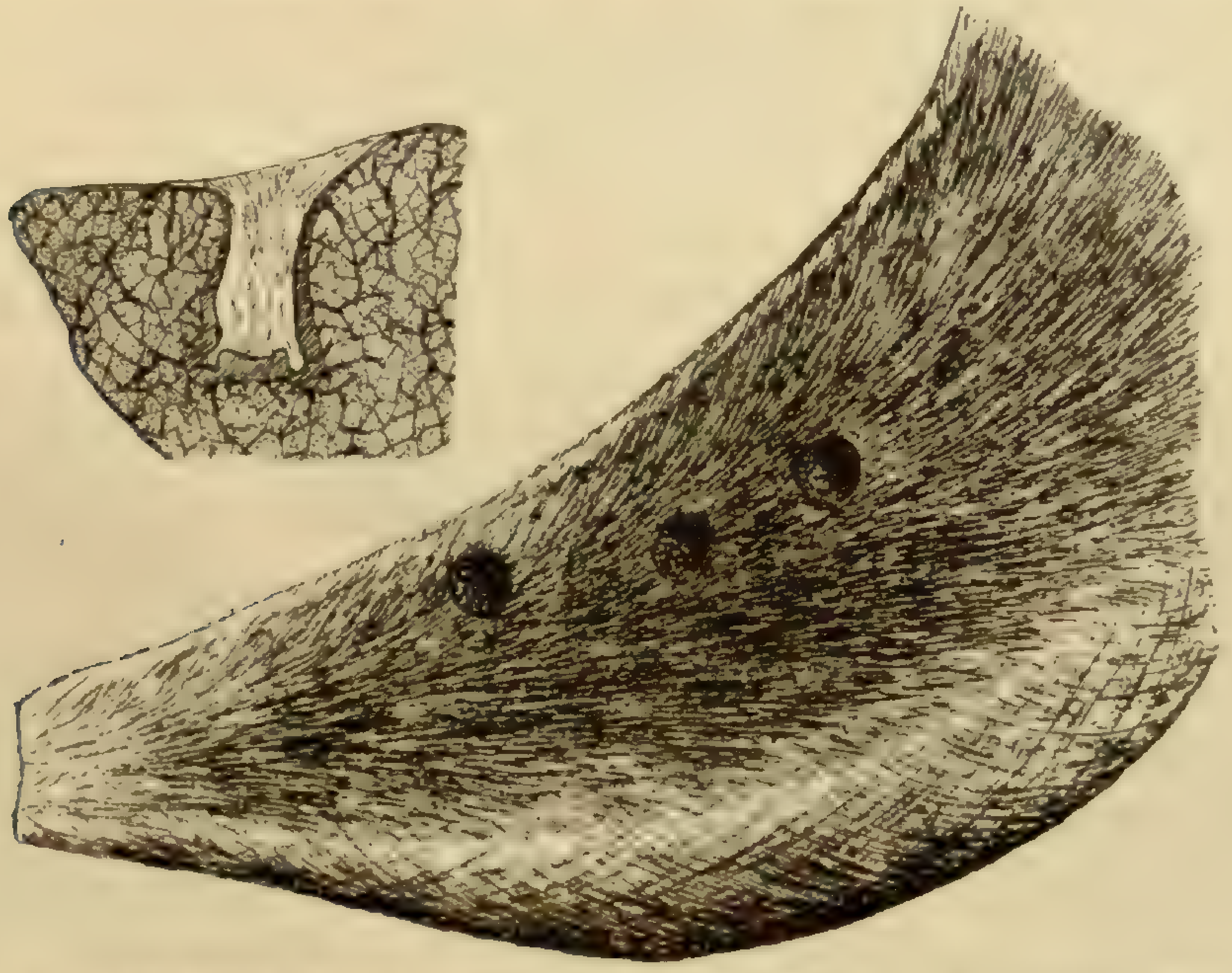

FIG. 1. The shoulder of a sheepshead with three depressions from which the leeches have been removed and one of the depressions cut in two lengthwise.

cidentally crowds the sucker down into the tissues of the fish, so that, in time, this depression may reach into the underlying muscles to a depth of half an inch or more and have an opening of about a quarter (or less) of an inch in diameter. The bottom of the depression has a larger diameter. Fig. 1 represents the positions of three depressions from which the leeches have been removed, and one of the depressions cut in two lengthwise.

These leeches are capable of becoming greatly contracted, and when one is disturbed it draws back until it appears as a mere brownish pyriform knob which entirely covers the place of attachment.

The burying of the posterior segments in the tissues of the host has brought about an interesting structural change so that we find the anal opening shifted forward to a position between somites XXIII and XXIV instead of between somites XXVII and XXVIII, as in the other members of the genus. It is noticeable that, while the young leeches whose posterior portions are not yet deeply imbedded have the characteristic position of the anus (XXIII–XXIV), the outline of the posterior part of the body is still a regular curve showing none of the pedicular characteristics so pronounced in the older individuals. The posterior sucker, however, is very strongly developed even in those not more than a centimeter long.

Practically nothing is known of this leech separate from its host, but it seems possible that a part of its existence may be spent elsewhere. During September, 1903, I examined several thousand fish of this species from Lake Pepin and found only three isolated leeches, each about a centimeter in length. The posterior sucker, while imbedded in the tissue, was not sunk in deeply and so had not produced the characteristic peduncle. They were evidently young ones which had recently attached themselves to their hosts and were gradually sinking the posterior sucker into the host's flesh. As full grown specimens, deeply imbedded, were found in the same locality during August of 1899, at least some of the adults must remain with their hosts during the summer and probably throughout the year.

Description[2]

Like *Placobdella parasitica* and *P. rugosa*, this is a species of large size, though not quite equaling the largest

[2] This description is based upon both young and large mature specimens gorged with blood. In view of unavoidable delay in the publication of Professor Nachtrieb's projected report on the leeches of Minnesota, Professor Moore kindly consented to the free use of his description prepared for the systematic portion of the report here alluded to. I have retained the specific name suggested by Moore, though his description, being based upon a single large, gorged and much contracted specimen, was of necessity somewhat incomplete.

examples of the forms mentioned. It is more than usually contractile and therefore difficult to preserve in a suitable condition for study. The outline is very characteristically pyriform and strongly convex dorsally, as shown in the figures. But the most striking peculiarity is the attenuation of the posterior somites to form a narrow pedicel just in front of the posterior sucker, which consequently stands out freely in a most characteristic manner. The oral sucker has the same structure as in *P. parasitica.*

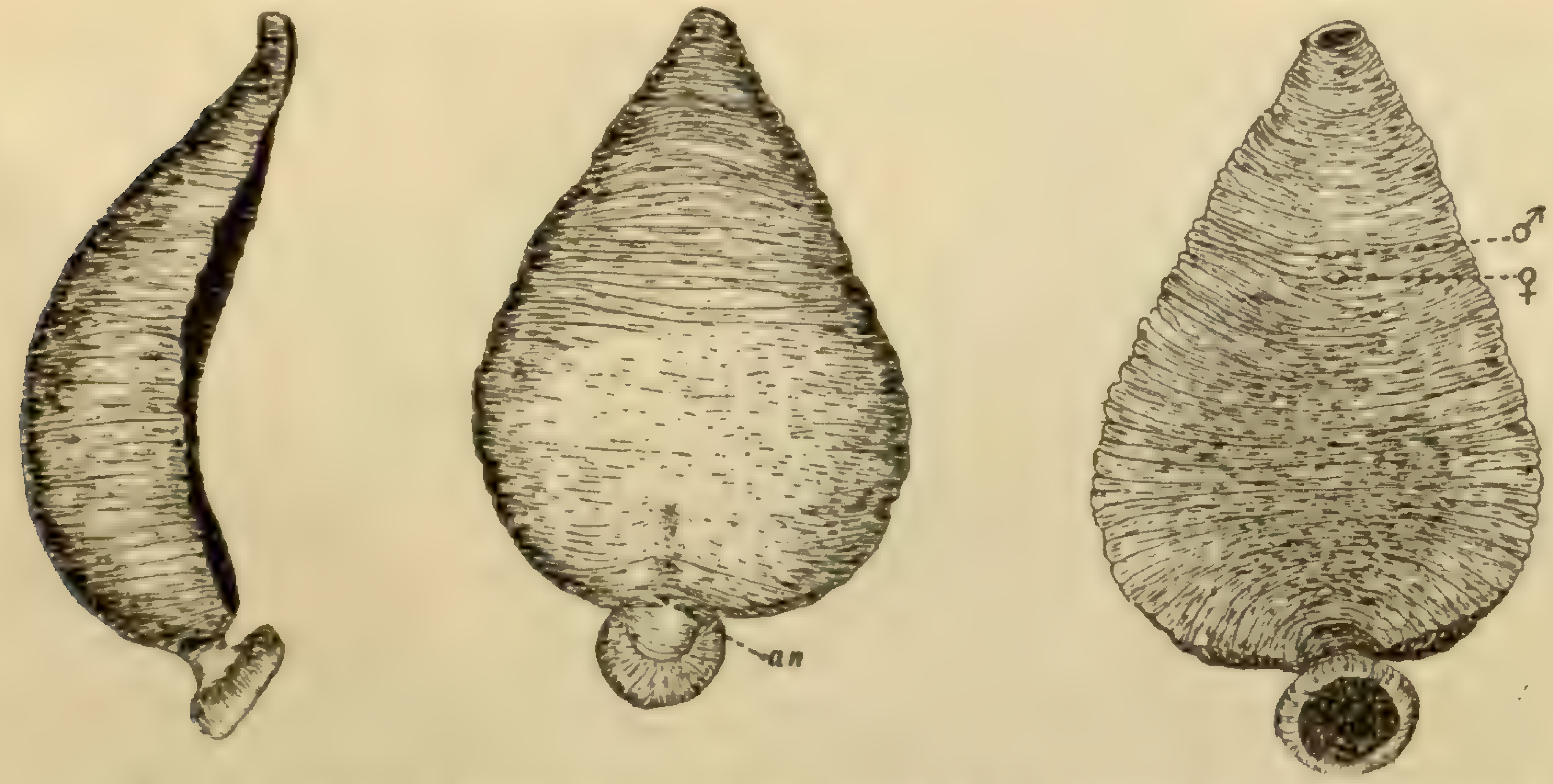

FIG. 2. Lateral, dorsal and ventral views of a mature specimen gorged with blood.

No trace of cutaneous papillæ can be detected, the skin being perfectly smooth. The segmental sensillæ and scattered sense organs are very indistinct. Eyes are very difficult to detect in the mature animals, but appear as small pigment masses at III–IV in the young. The annulation is essentially like that of *P. parasitica* excepting the caudal peduncle and the generally simpler structure of the corresponding somites of *P. parasitica.*

Somites I and II contain each but one annulus. Somites III and IV are biannulate and V is biannulate dorsally, but ventrally the furrow fades away medially. VI is triannulate above, but the furrow a1–a2 is incomplete below. Somites VII to XXIV are triannulate, but

the furrow a1–a2 is incomplete medially on the ventral side of both VII and VIII, and in most of the succeeding sonites is less marked than either a2–a3 or the intersegmental furrows. In the anterior somites and to a less degree in the posterior, a3 is slightly longer than a1 or a2. The annulation of the post-anal somites, constituting the caudal peduncle, is irregular and somewhat puzzling on the older specimens, but is fairly distinct on the younger ones. Somite XXIV, which immediately succeeds the anus, is triannulate. Somites XXV, XXVI and XXVII are all biannulate, but a1 of somite XXV is partially divided and a1 of both XXVI and XXVII is

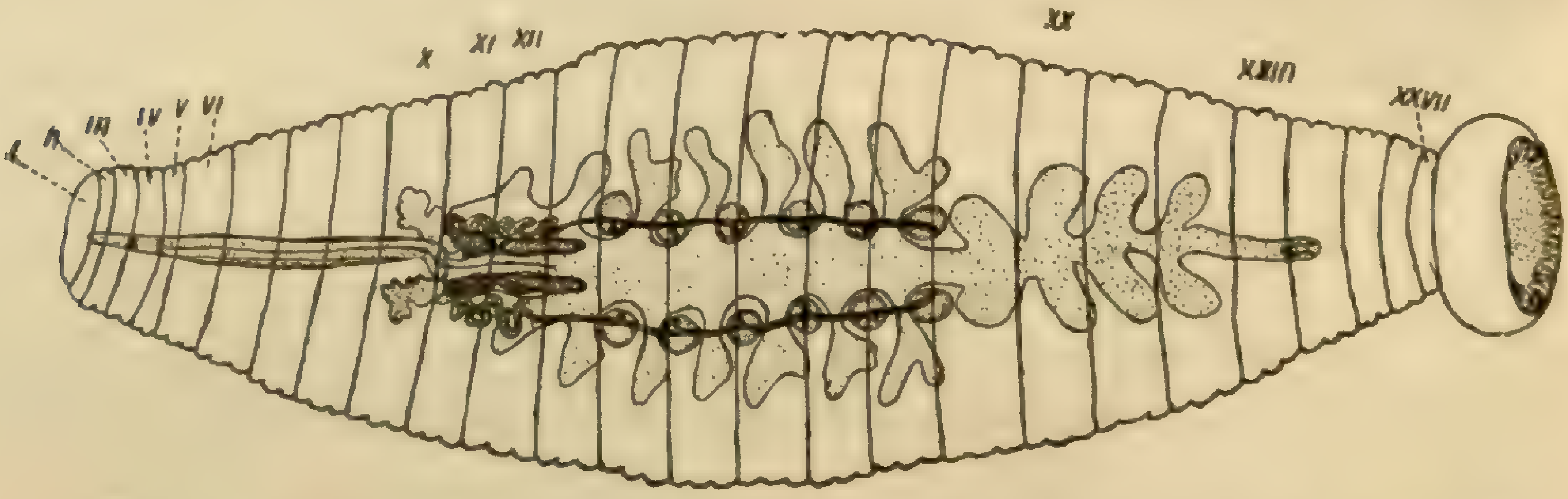

FIG. 3. Sketch of a young specimen showing somites I–XXVII, annuli and relative positions of the eye (*e*), proboscis (*prob*), esophageal gland (*oeg*), enlarged portion of the vas deferens communis (*s*), ovary (*ov*), testes (*T*), vas deferens communis (*vdc*), intestine (*int*) and anus (*an*).

larger than a2. Neither annulus of XXVII is complete, a1 reaching only to the sides of the body and a2 not as far. The disc is composed of somites XXVIII to XXXIV. The accompanying Fig. 3 represents the arrangement of the furrows in a young animal. Somite XXIV is the last segment of the body proper and its posterior boundary forms in contracted specimens a fold which envelops the contiguous portion of the narrowed peduncle. The latter continues to narrow to the sucker, to the middle portion of which it is strongly attached for rather more than the posterior half. The posterior sucker is larger, circular and directed strongly ventrad. The nephridiopores are in the sensory annuli of somites VIII to XI and XIII to XXIII and are placed similarly to those of *P. parasitica.*

The mouth is very small and situated far forward near the anterior rim of the sucker in somite II. As in related species, the proboscis is slender and the crop is provided with seven pairs of large cæca reaching nearly to the margins of the body. The cæca, however, are less deeply and finely divided than in *P. parasitica,* each of the first six pairs exhibiting only two or three rather short lobes. The intestine reaches to the posterior part of somite XXIV or even beyond and then bends abruptly forward toward the dorsum as an extremely narrow rectum reaching to the minute anus situated at XXIII–XXIV. The forward curvature of the rectum and the anterior position of the anus are unique features in the family. The salivary glands are widely scattered through the anterior two thirds of the body. On either side of the esophagus in somites X and XI lie a pair of compact esophageal glands which join the esophagus by a short duct in somite XI.

The reproductive organs are essentially similar to those of *P. parasitica.* The male and female external orifices are situated at XI–XII and XIIa2–a3, respectively. Six pairs of testes are crowded between the bases of the gastric cæca. The large sperm sack and the ejaculatory duct of the vas deferens form a compact snarl in somite XII in the immediate neighborhood of the atrium. Nothing is known of the early stages of development.

MARINE LABORATORIES, AND OUR ATLANTIC COAST

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WE are fortunate above all civilized nations in having in the range of our Atlantic sea-board a unique diversity of conditions affecting marine life. The arctic current creeps down the northern New England coast to Cape Cod, and during the winter the strong northeasterly winds drive its cold waters southward to the mouth of the Chesapeake. In summer, however, the southerly winds reverse these conditions, and the warm surface waters from the Gulf stream are drifted upon the shores between Cape Hatteras and the southern side of Cape Cod.

Another well-marked region is that between Cape Hatteras and Cape Canaveral, Florida, where we find a very characteristic warm-water fauna, which is again distinct from that of the coral reef region of Florida, south of Miami.

Thus, broadly speaking, there are four well-marked faunistic regions along our coast, and each affords its own peculiar problems for research. A mainly arctic fauna is found from northern Maine to Cape Cod, a transitional and seasonally fluctuating fauna from the southern coast of New England to Cape Hatteras, creatures of a warm sea from Cape Hatteras to Cape Canaveral, Florida, and a strictly tropical colony from Biscayne Bay, Florida, southward.

The physical features of the coast itself are also most important in determining the character of the animals of the shore. Thus the rocky wave-worn ledges of the coast of Maine, the varied character of that of southern New England, the monotonous stretch of shifting sand be-

tween Sandy Hook and Cape Canaveral, and the coral reefs of Florida, have each their own peculiar fauna and impose their own limitations upon the diversity of animal life. A diversity which is accentuated by the fact that in Florida we find a tidal rise and fall of less than two whereas in northern Maine the diurnal range is more than thirty feet.

Moreover, the relatively brackish and protected waters, such as those of Long Island, Pamlico and Albemarle Sounds, Chesapeake and Delaware Bays, and the tortuous estuaries and salt-water creeks of the Carolinas and northern Florida, have faunæ differing widely from those of the more richly endowed outer sea-beaches.

It is therefore evident that in so far as research is concerned no one biological laboratory can grant facilities other than those limited by the conditions of its own locality. The purposes of research demand that we establish a series of stations at salient points from Maine to southern Florida.

On the other hand, the successful prosecution of research demands that our youth be trained to its performance, and to this end it is essential that certain of the more centrally situated laboratories should devote some part of their energies to the giving of primary instruction.

Such instruction should, I believe, be given only in those laboratories which are placed near large centers affording the advantages of accessibility and diversity of intellectual interests. On the other hand, a certain remoteness from the busy world and consequent freedom from interruption is peculiarly favorable to the conduct of research, and it is interesting to observe that the only laboratory, along our coast, devoted exclusively to research is placed upon the most inaccessible island along the entire range from Maine to Florida.

At present we find one laboratory at South Harpswell, Casco Bay, Maine, a great center at Woods Holl, another at Cold Spring Harbor, in Long Island Sound, another

at Beaufort, North Carolina, and one at the extreme westerly and southerly end of the Florida Keys.

No laboratory has as yet been established along the interesting coast between Hatteras and Sandy Hook, with its peculiar transitional fauna; yet such situations as Cape May, or Linhaven, or Willoughby Harbors in Hampton Roads, would afford a suitable site for such a station.

It is not so remarkable that no laboratories have been established upon the inner shores of Delaware or Chesapeake Bays, or at Pamlico or Albemarle Sounds, for in these brackish inland waters the fauna is but limited in comparison with the rich variety of forms to be found along the exposed sea-beaches. In future, indeed, we should endeavor to avoid the error which has, in places, been made of building our laboratories in situations from which the open water is not readily accessible at all times, for it is peculiarly true of every laboratory that the animals which afford the subjects of its most significant researches are invariably those which may be obtained in abundance in the near neighborhood of the station itself. It is, therefore, most desirable that the laboratory be placed in close proximity to the richest collecting grounds of the region.

It is remarkable that so little effort has been made to properly install a laboratory for general instruction and research upon the coast of New England north of Cape Cod Bay. Yet here we find one of the most sharply differentiated of the faunistic divisions of our coast. The welfare of research in marine biology demands the adequate maintenance of such a station.

Returning recently from a visit of half a year to various biological centers in Europe the writer has formed the impression that the scientific results which have been achieved by investigators in our marine laboratories have won the admiration of European students, while at home our intelligent public is only beginning to awaken to the fact that they are worthy of respect.

In America, however, we may consider it fortunate that in order to win that form of recognition which leads to advancement in material as well as in intellectual well-being, it is necessary that our institutions of learning should attract the respectful interest of broad minded men of culture who are also leaders in the great affairs of the commercial world. Much may be learned by those desirous of furthering the already superior work of our laboratories, through a study of the methods of management of the great museums of New York City. Certain it is that the direction of any successful laboratory demands a two-fold capacity. On the one hand, we face a problem of expenditure and receipts, and on the other hand, a dependent but widely different problem of the scientific scope and aim of the institution. A neglect to attain to excellence of management from the purely commercial standpoint, must react unfavorably upon the ability of the institution to attain toward the realization of its proper ideals in scientific achievement. It appears to the writer that our institutions of learning which are dependent upon the public for support owe it as a duty to publish annually a clear, detailed and perfectly intelligible financial statement. Surely funds devoted to the giving of instruction or the prosecution of research can not be too carefully accounted for or too wisely expended.

It is unfortunate that throughout the length of our great Atlantic seaboard there is no situation well suited to the establishment of a marine laboratory which may remain active throughout the year. In winter the frozen harbors of the north, the relative inaccessibility and desolation of the Carolina shores, the hurricane season of Florida interpose practical barriers to the plan of maintaining any one of our stations constantly open. We have no Naples with its brilliant bay, its genial climate, and over it as a veil the association of history deepening every charmed impression of its beauty.

BIOMETRY AS A METHOD IN TAXONOMY[1]

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We take it for granted that the systematic description of plants, and animals, is not the province of the amateur, however interested he may be in a special group of living things. To the contrary this work should be done by the professional botanist, or zoologist, and demands a high grade of trained skill and judgment. More intelligence is needed than suffices to carefully fill out a card for a catalog, and yet how often do we find descriptions of species that would be discreditable to even a librarian's assistant!

The characters of one species are sometimes described as "smaller," "longer," "darker" or "lighter" than those of another, but upon reading the description of the other species referred to, the characters are again equally lacking in exactness. It is useless to enlarge upon this item, for every naturalist is sadly familiar with such imperfect and inadequate descriptions.

Biometry offers a method of great value for the study of specific characters, and the consequent clear and definite statement of the results of such study. There are workers either frightened at the mathematics of the method, or scornful of the whole thing on the general principles of conservatism, or prejudice. The mathematics of biometry, considered merely as a biological working method, is that of simple arithmetic, with no operation more complicated than the extraction of the square root.

It is certainly of great advantage to record in the standard deviation an exact mathematical statement of the variability of a character in place of the sometimes ut-

[1] Read at the Seventh International Zoological Congress, Boston, August, 1907.

terly meaningless, or again only partly useful, qualitative phrases which may be given. The correlated variability of some of the characters is important. Descriptions based on the mean and range of variation of each character and so expressed are better than those based on values taken here and there at random and then, when once published, petrified into a specific type ideal. A naturalist later tries to identify a specimen with this very limited description, but the characters of the specimen are too divergent and so a new species is created. Still later another naturalist works with a hundred specimens, including the characters given for the two preceding species, and then synonymy is born and with it trouble forevermore.

As an illustration of the usefulness of biometry for the solution of taxonomic problems I may take the case of the common Florida-Caribbean holothurian described in 1851 by Pourtalès as *Holothuria floridana*. In 1868, Semper considered this species identical with *H. atra* Jäger, 1833, from the Celebes. All authors have followed Semper to the date of my publication (1905). In the meantime Ludwig, in 1883, recognized a species in the West Indies different from the Indo-Pacific form and failing to identify it with *H. floridana* Pourtalès, created a new species, *H. mexicana*. The same error was repeated by Theél, in 1886, in making his *H. africana*.

With a feeling that things were not as currently accepted, I concluded to apply the method of biometry to this problem. From the United States National Museum, Harvard University, and my own collections, 138 specimens, covering nearly the whole geographical distribution of the two species were available for the work. In the solution of the general problem before me no attempt was made to determine place modes of which, in minor details, there were sometimes indications. Every important character was submitted to statistical study and the result is that *H. floridana* Pourtalès is reestablished as a valid species, with *H. mexicana* Ludwig and *H.*

africana Theél as synonyms. The old characters have been redefined, new ones added, and those differentiating *H. atra* and *H. floridana* clearly stated. The young and old have been segregated and differentiated and the results of growth determined. The nature and extent of the variation of each character has been recorded. An entirely new character for holothurians has been discovered in what I have called "pits," in the body-wall of *H. atra*.

It is not possible in taxonomic work to give several years to the study of each species and it often happens that the material is not sufficient. If an author will make a thorough biometric analysis of the characters of at least one species in his group, he will gain a rare insight into the relative values of the characters. The method is searching and leads to especial carefulness in investigation and statement. Even if one has not an ideal number of specimens his determinations are checked by their probable errors. In the case of some characters, as for instance, the spicules of holothurians, an abundance of material is present in each specimen. More and more of the anatomy becomes involved as the work progresses. Now that the individuality and continuity of the chromosomes has been demonstrated, McClung has suggested that their number and grouping constitute family, generic, and specific characters of just as definite worth as those that heretofore have been employed. The more characters studied the better, and the ideal taxonomy will be based upon the whole life-history. Then the error of describing the young and old of a species as independent species will not be repeated.

It naturally follows from biometric analysis that a group of individuals, giving as much as possible of the range in variation, should be established and deposited, preferably in a national museum, as the specific type group rather than some arbitrarily selected type specimen. We have instances of specific descriptions based upon one individual, with an apology by the author for

the lack of anatomical details because he could not dissect the one precious specimen!

The best way to avoid trouble in taxonomy is to begin with making the original description as complete as possible. It is then a simple matter to condense for practical diagnostic purposes. The biometric determination of the variability of the different characters allows of their arrangement in the order of increasing variability and will perhaps demonstrate which are the "best" characters. It is too soon to state exactly what percentage of divergence justifies the creation of a variety, or of a species, and it is not probable that any universally applicable measure will be established.

Biometry gives us data of value bearing upon one or more of the factors of evolution and records them in the best form for use. We know that under varying environmental conditions different varietal, or specific forms respond. The new forms may be only temporary and followed by still other new forms, under other changed conditions, or with reversion, when the old conditions are restored. Characters, whether expressed in the terms of biometry, or not, are not permanently fixed by the publication of a specific description. It is to be hoped that the spirit of Darwin is with us yet and that we realize that species are in a state of evolution, either continuously or discontinuously, slowly or rapidly. If we are to follow species in their evolution we must have exact and comprehensive statements of their characters from time to time as it is possible, and, if in the terms of biometry, these statements are always in harmony and comparable.

If then, while performing the necessary work of taxonomy, we can make our descriptions more complete and nearer the truth; if occasionally we may be relieved of the necessity of creating a new species; if our work may contribute to the advancement of the philosophy of biology, should we not welcome biometry as a method which can well serve in one and all of these things?

SHORTER ARTICLES AND CORRESPONDENCE

THE GENUS PTILOCRINUS[1]

Mr. F. A. Bather has just made known a second species of the interesting genus which I described a year ago[2] under the name of Ptilocrinus; his material was obtained in 70° 23′ S. lat., 82° 47′ W. long., at a depth of about 480 meters; the color of the animal in life is recorded as "flavus brilliant."

The type species of Ptilocrinus, *P. pinnatus,* came from the Queen Charlotte Islands, off British Columbia, and was dredged at a depth of 1,588 fathoms, about six times the depth at which *P. antarcticus* was found.

Although at first sight, perhaps, it is somewhat surprising that the two known species should be found so far apart geographically and bathymetrically, if we look closely into the matter we find that it is quite what we should expect. Geographically and bathymetrically the recent crinoids are divisible into three well-marked faunæ: (1) the Indo-Pacific-Japanese, characterized by the families Zygometridæ and Himerometridæ, the genera Comatula, Phanogenia, and most of the species of Comaster in the Comasteridæ, the genera Ptilometra, Asterometra, Calometra and one of the two species of Tropiometra of the Tropiometridæ,[3] and the genera Perometra, Nanometra, Compsometra, Thysanometra and Iridometra of the Antedonidæ; among the stalked crinoids Metacrinus, Carpenterocrinus, Hypalocrinus and Phrynocrinus are only known from this region; (2) the Polar-Pacific, including the Arctic and Antarctic circumpolar areas, and the entire American coast of the Pacific from Bering Straits to the Straits of Magellan, the coasts of eastern Asia to southern Japan (where it meets the preceding at Tokyo Bay), including the Sea of Okhotsk and the Sea of Japan, and the Atlantic coasts south to near the Hebrides and the Faroë channel, and to the

[1] *Ptilocrinus antarcticus* n. sp., a crinoid dredged by the Belgian Antarctic Expedition. *Bull. de l'Acad. roy. de Belgique* (classe des sciences), No. 3, mars, 1908, pp. 296–299, fig. p. 299.

[2] *Proc. U. S. Nat. Mus.,* XXXII, p. 551, fig. 1, p. 552.

[3] The second species, *T. carinata,* appears to have recently extended its range into the Atlantic.

Gulf of Maine, characterized by various genera belonging exclusively to the Antedonidæ, Heliometra occurring everywhere, Hathrometra confined to the north, and Isometra to the south, while Thaumatometra occurs in the south, but extends northward in the Pacific to the Aleutian Islands; among the stalked crinoids the *Bathycrinus carpenterii* type (*B. carpenterii, B. complanatus* and *B. australis*) appear possibly to be peculiar to the region; bathymetrically, the characteristic forms (except Bathycrinus) are inhabitants of comparatively shallow water in both polar areas, but dip downward to a considerable depth when passing under the tropics; and (3) the Oceanic, which occurs everywhere in moderate to very deep water with the Indo-Pacific-Japanese, and extends thence over the entire ocean area, *except* that it does not intrude into the area occupied by the Polar-Pacific; the characteristic forms are the species of Thalassometra having rounded and spiny rays and arm-bases (such as *T. bispinosa, T. villosa, T. gigantea, T. pubescens, T. multispina* and *T. aster*) and certain other species, such as *T. flava, T. porrecta* and *T. magnicirra*, Stylometra, Bathymetra and Charitometra, except the *aculeata, hepburniana, basicurva* and *tuberosa* groups; of stalked crinoids, Rhizocrinus, Endoxocrinus, and the species of Bathycrinus, except the *B. carpenterii* group, belong here; the West Indian fauna falls almost wholly in the last division, but there is a trace of Indo-Pacific-Japanese influence, as, however, we might expect, since the entire Oceanic fauna is a direct, though considerably modified, derivation from it, even the well-known subgenera of Pentacrinitidæ, Encrinus[4] and Isocrinus being only a comparatively slight advance over the apparently more primitive Metacrinus type. The Mediterranean—northeast Atlantic fauna, characterized by Antedon (*A. mediterranea, A. bifida* and *A. petasus*) and Leptometra, appears to be a localized offshoot from the Polar-Pacific.

Bearing these facts of distribution in mind, we are not surprised to find Ptilocrinus where Mr. Bather found it, for it appears to be a genus of the Polar-Pacific area, and the same *may* be true of Calamocrinus. Although Heliometra occurs throughout this area, the two arctic species, *glacialis* (= *eschrichtii*) and *quadrata* (with their representatives in the Sea of Okhotsk, *maxima* and *brachymera*) differ from the Antarctic and east Pacific species in the smoothness of their arms, and in

[4] The subgenus Cenocrinus of Wyville Thomson.

a different distribution of the brachial syzygia; we find, therefore, that the entire Pacific portion of the Polar-Pacific area, from Bering Straits to the Antarctic Ocean, is really an extension of the latter division of the Polar-Pacific area northward; so that, had we reasoned backwards from the facts at hand before the appearance of Mr. Bather's paper, we might very well have prophesied the discovery of a Ptilocrinus in the Antarctic regions.

Mr. Bather remarks that I did not publish a generic diagnosis when I established Ptilocrinus; I did not, for the reason that in a monotypic genus, we are quite unable to say which are generic and which specific characters, and to tell in what way a new species will differ from the type; it is all right to indicate the differences provisionally between a new monotypic genus and older genera, but drawing up a diagnosis of a new monotypic genus implies rather more of a proprietorship over the animal kingdom than I am willing to assume.

AUSTIN HOBART CLARK.

UNITED STATES BUREAU OF FISHERIES.

A NEW RHINOCEROS FROM THE LOWER MIOCENE OF NEBRASKA[1]

Among several animals found by the writer at Agate, Sioux Co., Nebraska, in the spring of 1905, was a new form of hornless rhinoceros.

The type (No. HC105, collection of the writer) consists of a complete skull, the posterior portion of the left jaw, the atlas and the axis. This description has been delayed, hoping additional material might be secured.

The specimen was found in an exposure of the Dæmonelix Beds, about four miles west of the well-known Agate Spring Fossil Quarry, on the ranch of James H. Cook. The bone horizon in this quarry is practically, if not identically, the same as that in the Agate Spring Quarry. Strictly speaking, the Dæmonelix Beds are an integral part of the Lower Harrison Beds, forming the upper portion of them.

Associated with this specimen were the remains of Syndyo-

[1] Extract from a paper read before the American Society of Vertebrate Paleontologists, December 29, 1907, at New Haven, Conn.

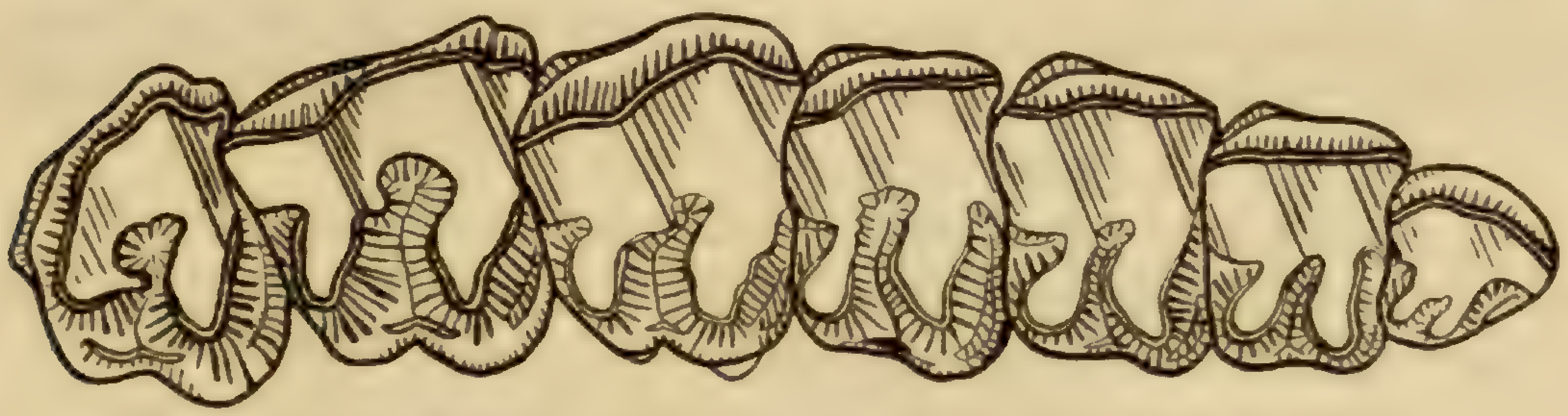
ceras, Miolabis, Merychyus, Thinohyus, Parahippus, Moropus, Brachypsalis and other animals.

The specimen is referred to the genus Aceratherium, and the specific name of *egregius* is proposed. It is separated from its contemporary Diceratherium, by the absence of horn cores, or

Aceratherium egregius Cook. ¼ natural size.

any trace thereof on the nasals; by a relatively longer and proportionately narrower skull; by a larger first upper premolar, and by many minor features.

The nasals are broad and flattened posteriorly, narrowing rapidly anteriorly, and extending about one half inch in front



Molar-premolar Series. Right side. ½ natural size.

of the premaxillaries. The temporal ridges unite in forming a sagittal crest, which rises quite abruptly, adding materially to the general saddle-shaped appearance of the skull.

A more complete report will appear in volume three of the Nebraska State Geological Survey.

MEASUREMENTS

	Mm.
Greatest length	473
Extreme width across zygomatic arches	245
Distance between orbits across frontals	140
Width of brain case	90
Length of upper molar—premolar series—left side	202
Length of upper molars, left side	95
Length of lower molars, left side	100
Length of diastema P. 1 to incisor	61

HAROLD JAMES COOK.

THE UNIVERSITY OF NEBRASKA,
March 1, 1908.

NOTES AND LITERATURE

PLANT CYTOLOGY

Some Recent Research on the Cilia-forming Organ of Plant Cells.—The blepharoplast, or cilia-forming organ of plants, is present in the sperms and other motile gametes and in the zoospores. When fully developed it lies close against the plasma membrane of the cell in the form of a granule or band of various shapes to which the cilia are attached. The origin of the blepharoplast has been the subject of considerable research with conflicting conclusions.

Strasburger in 1900 from studies on the zoospores of Œdogonium, Cladophora and Vaucheria decided that the blepharoplast arose in the plasma membrane (Hautschicht), the nucleus lying in close proximity at the time of its formation; Mottier later described a similar origin for the blepharoplast of Chara. In sharp contrast to the above conclusions are those of Belajeff from studies on the sperms of certain pteridophytes, Ikeno for Cycas and Marchantia, and Hirasé for Ginkgo, who hold that the blepharoplast is an attractive sphere or centrosome. Belajeff in particular has consistently described the blepharoplast as occupying, as a centrosome, the poles of the spindle in the mitosis previous to the formation of the sperm mother cells, and has held that the blepharoplasts of Marsilia came from centrosomes passed on from the previous mitoses; each sperm mother cell being thus supplied with a blepharoplast. Ikeno, especially from studies on Marchantia, also holds to the centrosome nature of the blepharoplast, but his conclusions are disputed by Miyake. A third group of investigators to which Davis and Yamanouchi also belong (as will be noted from the reviews which follow) have described the blepharoplast as arising in the cytoplasm while the nucleus is in a resting condition, and as holding no genetic relation to any preceding mitoses. Thus Webber from very thorough studies on the cycad Zamia described the blepharoplasts as developing *de novo* on opposite sides of the nucleus and at some distance from it before the mitosis that precedes the differentiation of the sperm nuclei; Shaw for Marsilia also

claimed that the blepharoplasts did not occupy the poles of the spindle in the final mitosis, as would be expected of a centrosome-like body.

These divergent views have great theoretical interest in relation to the subject of the polar organization of cells reviewed in the July number of the NATURALIST. Zoospores invariably present a conspicuous polarity since their cilia are situated at one end or at a definite point on the side, and while the complex coiled structure of many sperms obscures this polar organization the process of blepharoplast development is always from a region which is clearly a pole of the cell. Indeed, these types of cells present some of the best illustrations of complex polar organization. Perhaps the most vital problem of zoospore formation and spermatogenesis is then the question whether or not the polar organization of these cells arises *de novo* at the time of their development or is handed on from the succession of cells which are their progenitors.

Davis[1] found in the zoospores of Derbesia a very interesting subject for the study of a remarkable blepharoplast. Derbesia is a marine green alga in the group of the Siphonales, distinguished from other forms in the same group by having very large zoospores, each of which is provided with a circle of numerous cilia. These zoospores are developed in a large sporangium which contains at first several thousand nuclei, but a process of nuclear differentiation begins very shortly in the young sporangium; certain of the nuclei increase in size while the great majority begin to degenerate and finally break down. The large surviving nuclei become distributed rather uniformly throughout the protoplasm of the sporangium, and each is evidently the center of dynamic activity for the cytoplasm in its vicinity. This is indicated by the arrangement of numerous conspicuous protoplasmic strands which radiate from the nucleus between the surrounding plastids.

The segmentation of the protoplasm does not begin until the process of nuclear degeneration is practically ended, and the sporangium contains only the larger nuclei (from 30–300), which are to take part in spore formation. Cleavage furrows start from the periphery of the sporangium and cut into the protoplasm in the form of curved and branching furrows.

[1] Davis, B. M. Spore Formation in Derbesia. *Ann. of Bot.*, XXII, p. 1, 1908.

These at first mark out large areas, which, however, become successively smaller as new furrows are formed at the periphery or strike off from the sides of the older ones. Finally the protoplasm of the sporangium becomes divided into approximately equal masses around the large surviving nuclei. These masses are the zoospore origins and each develops into a uninucleate zoospore.

The nucleus first lies at the center of the zoospore origin, with protoplasmic strands radiating out in all directions among the plastids. Granules are present at the bases of the protoplasmic strands close to the nuclear membrane. The nucleus then moves somewhat towards the periphery of the cell and it becomes clear that the protoplasmic strands on that side at least actually extend to the plasma membrane; these strands become arranged in the form of a funnel with the broader end against the plasma membrane. With this stage the zoospore origins clearly exhibit a polar organization.

A circle of granules, which is nearly twice the diameter of the nucleus, now appears where the broader region of the funnel-shaped arrangement of strands meets the plasma membrane. From earlier stages it seems probable that these granules pass along the strands as organized bodies from the neighborhood of the nucleus; they certainly arise within the cytoplasm. The granules in the circle finally fuse with one another to form a firm ring, which lies in the plasma membrane or just under it; this ring is the belpharoplast. The blepharoplast later splits into two rings, one immediately below the other, and the circle of numerous cilia grows out from the lower. The nucleus finally returns to a position near the center of the cell.

The most important points to be noted in this history of the origin of the blepharoplast in Derbesia are as follows. *First*, it seems clear that the nucleus is concerned in a most intimate manner with the development of the blepharoplast, since the numerous granules, which form the ring, appear to come from near the surface of the nucleus and travel along the radiating strands arranged in the form of a funnel; the elements forming the blepharoplast are not developed in the plasma membrane. *Second*, these very numerous granules can not be centrosomes and bear no relation to mitotic figures for there are no nuclear divisions in the sporangium. *Third*, the polar organization of the maturing zoospores does not appear to be present in the

younger stages when the nucleus occupies a central position in the zoospore origin.

Yamanouchi[2] has given an account of spermatogenesis for Nephrodium in one of a series of papers dealing with the life history and apogamy of this fern. The blepharoplasts arise *de novo* just before the last mitosis in the antheridium, that mitosis which differentiates the sperm mother cells. They are first seen as small bodies lying within the cytoplasm on opposite sides of the nucleus and at a considerable distance from it; they appear suddenly, as differentiated by staining, and are unexpectedly large. The blepharoplasts move towards the nucleus and during the final mitosis take positions near the poles of the spindle. Sometimes the blepharoplasts may lie exactly at the poles of the spindle, and consequently suggest relationships to a centrosome, but this is not often, and there can be no such relationship in Nephrodium because centrosomes are not present in the earlier mitoses of the antheridium or at any other period of the life history.

As a result of the final mitosis in the antheridium each sperm mother cell receives one of the two blepharoplasts close by the side of the daughter nucleus. The nucleus in the sperm mother cell now increases in size and the blepharoplast, at first spherical, changes its form. It enlarges and is flattened somewhat against the side of the nucleus and begins to elongate. The outline becomes at first rhomboidal and then band-shaped as the blepharoplast gradually extends around the nucleus in the form of a semi-circular band.

A complicated development follows for both the nucleus and the blepharoplast. One end of the blepharoplast grows wedge-shaped and is loosely applied to the nucleus while the other end remains pointed and extends around in very close contact with its surface. The nucleus meanwhile changes its form, becoming a coiled structure and the elongating blepharoplast follows the coils in the form of a narrow band, which reaches to the end of the nucleus, and finally by extensive lateral growth covers the coil. In this manner the coiled and spiral form of the sperm is developed, and by this time numerous cilia have grown from the surface of the blepharoplast.

There is another structure in the sperm mother cell which

[2] Yamanouchi, Sh. Spermatogenesis, Oogenesis, and Fertilization in Nephrodium. *Bot. Gaz.*, XLV, p. 145, 1908.

must be briefly described. It appears as a minute body in the situation previously occupied by the central spindle of the final mitosis, and consequently far removed from the blepharoplast, which lies near the polar region of the spindle, with the nucleus between them. This structure is the "Nebenkern" of other authors. The "Nebenkern" later occupies various situations in the cell, but always remains as a small structure and does not enter into the construction of the spiral body of the sperm; it finally comes to lie in the cytoplasm which becomes attached, as a vesicle, to the posterior coil of the mature sperm.

Yamanouchi's results on Nephrodium are opposed to those of Belajeff for Marsilia, who holds that the blepharoplasts like centrosomes occupy the poles of the spindle and are derived from centrosomes in a previous mitosis within the antheridium. The account agrees with Webber's conclusions for Zamia that the blepharoplast arises *de novo* in the cytoplasm, and also with Shaw's view for Marsilia that the blepharoplast has no genetic relation to the pole of the spindle in the final mitosis.

It seems probable that the centrosome theory of the blepharoplast, as held by Belajeff, Ikeno and others, has placed undue emphasis on the proximity of the blepharoplasts, in the types studied, to the poles of a closely associated mitosis. There are no mitoses present during the entire period of zoospore formation in Derbesia, which consequently offers important evidence against this view. Since similar conditions are also present during zoospore formation in Œdogonium and a number of other algæ, the investigation of these types is likely to prove very interesting. The blepharoplast unquestionably gives a marked polarity to the cell, but it has not yet been established that this polar organization is derived, as such, from the immediate cell progenitors, however pleasing, for theoretical reasons, would be the establishment of such a history.

BRADLEY M. DAVIS.

ORNITHOLOGY

Riddle on the Genesis of Fault-bars and the Cause of Alternation of Light and Dark Bars in Feathers.[1]—In a much shorter paper

[1] Riddle, Oscar. The Genesis of Fault-bars in Feathers and the Cause of Alternation of Light and Dark Fundamental Bars. *Biological Bulletin*, Vol. XIV, No. 6, May, 1908, pp. 328–370, pls. xii–xv.

published in February, 1907, under the title "A Study of Fundamental Bars in Feathers" (*Biol. Bull.*, XII, 1907, pp. 165–174) the author gave a résumé of the results of studies here extended and for the first time fully set forth. The existence of "fundamental bars" in feathers was discovered by Whitman in the summer of 1902 (not published till 1907), who found them "to be common to all species of pigeons and birds in general," and that they "appear to mark all feathers of all species of birds."[2] The present research was undertaken at Professor Whitman's suggestion, whose observations furnished the starting point for these studies. These are: "First, there is in all feathers a 'fundamental barring' of the whole length of the feather; second, certain defects (fault-bars) occasionally appear in the plumages of birds reared under adverse conditions." The fault-bars are considered as regards (1) their morphology, (2) their extent and distribution, (3) their cause. Whitman's suggestion that fault-bars are due to malnutrition has been abundantly proved by experimental research. While normally due to lack of nutrition, they may be produced by feeding birds on Sudan III, by mechanical injury of the feather germs, by bad sanitation, parasites, etc., and by the use of amyl nitrite to reduce blood-pressure. From extended observation and experiment it has been determined that "fault-bars are normally laid down at night," when the blood-pressure is normally low. The interrelated facts bearing upon this assumption are thus stated: "(1) Diminished feeding of birds produces emphasized fault-bars. (2) Artificially reduced (amyl nitrite) blood-pressures produce equivalent defects. (3) The fault-bars are produced at night. (5) The lowest daily temperature in birds occurs from 1:00 A.M. to 5:00 A.M. (6) Other physiological conditions of the bird seem to be favorable at night for the production of low blood-pressures. (7) A lowering of the pressure would reduce the food-supply and have a tendency to produce defects."

Those parts of the feather which are grown under the poorest nutritive conditions are the so-called "fault-bars," while the intervening parts—normally the larger—are the result of the highest nutritive conditions, and form the "fundamental bars." The structurally weakened bars are also found to be less pig-

[2] *Bull. Wisconsin Nat. Hist. Soc.*, V, January, 1907, p. 13.

mented, although the difference in this respect between ''fault-bars'' and ''fundamental bars'' is not marked, but results in the melanin pigment being ''laid down in alternating light and dark transverse bars.''

Among the results summarized by the author as confirmed by or resting upon these investigations may be mentioned: The occurrence of fault-bars normally in all birds and in all feathers; they can also be produced experimentally. A daily blood-pressure rhythm with a minimum pressure between 1 and 5 A.M. ''The reduced nutrition brought about daily by this minimum blood-pressure; the disadvantageous position, in relation to the blood, of the pigment and barbule elements of the feather; together with the very rapid rate at which feathers grow, furnish the complex of conditions which bring unfailingly into existence a fault-bar, and to a more or less appreciable extent a light fundamental bar, at perfectly regular intervals in the entire length of every feather formation.'' ''The melanin pigment of the feathers of birds shows, under favorable conditions, quantitative variations of the pigment produced in response to changes in the available food supply. This is an additional evidence that this pigment is not a derivative of hæmoglobin, but of the serum or cell proteids.'' ''These results furnish a description, in the terms of physiology, of the mechanism of the 'inheritance' of certain fundamental color-characters of all birds.'' ''The fundamental bars furnish the starting point for all evolutionary studies on the color-characters of birds.''

These investigations may well serve as the foundation for researches upon the color-characters of birds, but whether they are to throw much light upon the genesis of color patterns in plumage remains for the future to disclose. It may be noted that no reference is made in this connection to the cause of differentiation of feather structure, treated by the author in a former paper.

J. A. A.

HERPETOLOGY

Ruthven's Variations and Genetic Relationships of the Garter-snakes.[1]—This paper of over two hundred pages, devoted to a

[1] Ruthven, Alexander G. Variations and Genetic Relationships of the Garter-snakes. *U. S. National Museum Bulletin* 61, 8vo, pp. xii + 301, with 82 text figures and 1 half-tone plate. Washington, Government Printing Office, 1908.

single genus of snakes, marks a new departure in North American herpetology in respect to methods of procedure. An attempt is made first to determine the value of the characters commonly employed in distinguishing the different forms of the group, as scutellation and color, through study of the normal range of variation in the number of dorsal rows of scales, number and arrangement of the labial and preocular plates, the number of the ventral and subcaudal plates, and the position and color of the stripes. All this is worked out with great care and detail for each form, so far as material is available, which includes about 3,000 specimens, gathered from throughout the known range of the genus. Distinction is made between individual, sexual and geographic variation.

The individual variation in the number of rows of dorsal scales, and the variation in the different forms of the group, is found to be due to the dropping out of certain rows. The law is thus stated: "The individual, geographic and racial variations in the number of dorsal scale rows in the garter-snakes is brought about by the shortening and loss of the same scale rows as are ordinarily dropped posteriorly in conformity with the taper of the body, and there is evidence that this decrease is due to a dwarfing of the body."

The cause of variation in the number of labial plates is not easily explained, but it is believed that there is good reason "for concluding that whatever the factors may be that influence the number of labial plates, the variations are geographic and have been the basis for the racial differences that now exist."

The color pattern in Thamnophis consists of three light longitudinal stripes—a median, and a lateral stripe on each side of the body—on a dark ground. They vary in width in different individuals of the same form, and also more or less in color. The median stripe is the most variable, and in some of the forms it is more or less obsolete. The lateral stripes are constant in position (in reference to the rows of scales involved), and as the position varies in different groups of forms it is available in diagnosis. Simple variation in color, however, has little diagnostic significance, owing to the wide range of individual variation within each form; "and, even when there are well marked geographic differences among forms, those in the same region tend to be similarly colored, as Allen has pointed out a number of times in mammals and birds, so that it is impossible to dis-

tinguish them sharply on this basis.'' Thus there is ''a marked increase in bright colors in the Pacific coast region in Washington, Oregon and British Columbia,'' and an increase in this same region ''in the amount of black pigment at the expense of the paler colors.'' ''A tendency toward a paler ground color and lighter stripes'' is noted in western Texas, southern New Mexico, southern Arizona and northern Mexico, and ''a tendency toward the production of red pigment on the Great Plains,'' and ''toward dark colors in the forest region of eastern United States.''

As a result of these detailed studies of variation and their probable causes and significance, the taxonomy of the group here presented is quite different from that of preceding authors. Only 19 ''forms'' are here recognized, in place of the 30 currently admitted by herpetologists. The author says:

"It may seem the extreme of 'lumping,' to assert that there are but four great groups or lines of descent in the garter-snakes, but I believe the evidence is sufficient to warrant the assertion."

These four groups are the *radix, sauritus, elegans* and *sirtalis* groups. He explains in a footnote (p. 39):

"It is best at the outset to ignore all questions of species and subspecies until their status is established, and to speak of these as forms. Forms, therefore, in the sense employed in this paper, are actual combinations of traits, having geographic extent, irrespective of whether they are isolated (species) or intergrade with their neighbors (subspecies). Detailed discussions of questions of nomenclature are also omitted, although the names are in every case the ones that, in the light of these investigations, we judge to be the right ones, following the International Code of Zoological Nomenclature. The proper name of each form will be found in the footnotes, together with the synonomy."

In the ''Table to illustrate the combinations of traits into forms, groups and divisions in the garter-snakes'' (pp. 40, 41), the ''forms'' and ''groups,'' and ''primary divisions'' (the latter simply numbered I and II) are listed, but it would have been a great convenience if he had given somewhere in his monograph a list of the ''forms'' with their full names as here employed. The form of nomenclature given in footnotes implies the provisional recognition of 12 species (binomials) and seven additional subspecies (trinomials), as follows:

1.	*Thamnophis megalops* (Kennicott).	*Radix* group.
2.	*Thamnophis marcianus* (Baird and Girard).	
3.	*Thamnophis radix* (Baird and Girard).	
4.	*Thamnophis butleri* (Cope).	
5.	*Thamnophis sauritus* (Linné).	*Sauritus* group.
5*a*.	*Thamnophis sauritus proximus* (Say).	
5*b*.	*Thamnophis sauritus sackeni* (Kennicott).	
6.	*Thamnophis angustirostris* (Kennicott).	*Elegans* group.
6*a*.	*Thamnophis angustirostris melanogaster* (Peters).	
7.	*Thamnophis scalaris* (Cope).	
8.	*Thamnophis phenax* (Cope).	
9.	*Thamnophis hammondi* (Kennicott).	
10.	*Thamnophis ordinoides* (Baird and Girard).	
10*a*.	*Thamnophis ordinoides elegans* (Baird and Girard).	
11.	*Thamnophis eques* (Reuss).	*Sirtalis* group.
11*a*.	*Thamnophis eques sumichrasti* (Cope).	
12.	*Thamnophis sirtalis* (Linné).	
12*a*.	*Thamnophis sirtalis parietalis* (Say).	
12*b*.	*Thamnophis sirtalis concinnus* (Hallowell).	

Of these groups he states (p. 186) that the *sirtalis* group "is without doubt the least diversified," since its members are given by most herpetologists only subspecific rank, owing to their evident intergrading.

Later on in the paper, in his "Discussion of Origins," he gives his reasons for believing that the genus Thamnophis had its origin in northern Mexico, and not in southeastern United States, as held by Cope and Brown. The four "groups" are each represented in northern Mexico and southwestern United States, and "each group is formed of a line of directly related forms, the extremes of which are very distinct," and these lines converge toward northern Mexico. He further states, under "Method of Evolution of the Forms" (p. 192): "If the range of the forms in the different groups of garter-snakes be carefully examined it will be found (1) that the different forms of the same group are found in different geographical regions, characterized by different environmental conditions; (2) that the area along the common boundary of two forms of the same group, where transition in characters takes place, is relatively

narrow''; just as has long been known to be the case in mammals and birds, and as Ortmann has recently affirmed to be the rule in crawfishes.

He considers that

"Experimental work alone can sufficiently reveal the influence of the environment upon the dwarfing and scutellation of these snakes. In the case of the garter-snakes, however, it should be noted: (1) That most of the forms are the result of dwarfing. (2) That the amount of dwarfing does not seem to be directly associated with the nature of the environment, for the form inhabiting a particular region is only slightly different from its nearest neighbor in the same group, while forms of widely different scutellation may inhabit the same region. Thus the conditions which apparently determine the scutellation of any form is the scutellation of its immediate progenitor, and the dwarfing it has itself undergone."

He believes that he is ''justified in concluding that the dwarfing is associated in some way with the environment.'' He then cites Allen's law (1876)[2] that the environmental conditions at the center of origin are most favorable for the existence of any group, and says:

"However this may be, the following facts will stand: (1) That the maximum scutellation and size in the genus Thamnophis occurs at the center of dispersal, and the forms that have been produced in the history of its migration have been formed principally by dwarfing and reduction in scutellation; (2) that the variation in the number of scales in the different series is definite and not promiscuous, and is correlated in a remarkable degree with changes in the environment. The development of the different groups has thus been orthogenetic."

He continues:

"From these facts it seems to me that the most tenable hypothesis of the evolution of the genus Thamnophis is that it originated and became differentiated into four main groups in northern Mexico. From

[2] ''In a general way, the correlation of size with geographical distribution may be formulated in the following propositions:

''1. The maximum physical development of the individual is attained where the conditions of environment are most favorable to the life of the species. . . .

''2. The largest species of a group (genus, subfamily, or family, as the case may be) are found where the group to which they severally belong reaches its highest development, or where it has what may be termed its center of distribution. . . .''—*Bull. Geol. and Geograph. Surv. Terr.*, Vol. II, No. 4, p. 310, July 1, 1876.

this region the groups radiated in all directions, but principally to the northward, and wherever they entered dfferent regions the changed environmental conditions acted as an unfavorable stimulus, which retarded growth, and differentiated the groups into dwarfed forms."

The first forty pages of this notable monograph are devoted to the taxonomy, distinctive features, and "variations" of the garter-snakes; the next one hundred and forty to a detailed account of the various "forms," including description, habits and habitat relations, range, variation and affinities; then follow about twenty pages of conclusions and general discussion, a bibliography of about 85 titles, and the index. The eighty-two text illustrations consist of diagrams showing the arrangement of the dorsal scale rows, the head plates, and the arrangement and numerical variation in the labial plates; diagrams illustrating the scale formula and its variations in the different forms; distribution as indicated by locality records (plotted on maps); and habitat views (half tones). It is altogether an excellent piece of work, which we hope to see emulated in other fields of taxonomic research, for which there is ample opportunity in the higher classes of vertebrates.

In his introduction Dr. Ruthven alludes to the "barrenness of general results" that has marked the systematic work in herpetology, due in part to the method employed, which has been "largely analytical in its nature, being for the most part descriptive of the existing diversities." While such work is important, it only makes known present conditions; as the author forcibly says, a knowledge of the processes that have brought them about is of the greater interest, since "systematic work can only become a true science when it seeks to formulate the laws involved in the history of the present forms. After analysis, therefore, as has been said, comes the need of a larger synthesis."

Dr. Ruthven's monograph strongly appeals to the present reviewer for two reasons: First, when curator of reptiles at the Museum of the Boston Society of Natural History some thirty years ago, he spent much time in trying to unravel the intricacies of variation in the garter-snakes, with a view to publication of the results, but other and more pressing interests intercepted the work; secondly, he repeatedly in the early seventies made strong appeals for the synthetic method in systematic work, and has published a large amount of data on individual,

sexual and geographic variation. Forty years ago systematic work was almost wholly analytic, and especially so in respect to the mammals, birds and reptiles of this continent. In my paper "On the Mammals and Winter Birds of East Florida, with an examination of certain assumed specific characters in Birds," etc., published in April, 1871,[3] the conclusions arrived at respecting "species" and specific characters are thus summarized:[4]

"(1) That the majority of nominal species originate in two principal sources of error, namely, (*a*) an imperfect knowledge of the extent and character of individual variation, and (*b*) of geographical variation. (2) That this imperfect knowledge is mainly due to the neglect of zoologists to study with sufficient care the common species of their respective countries, whence has arisen a faulty method of investigation and erroneous ideas respecting species and specific characters. (3) *Instead of the method at present pursued by a large school of descriptive naturalists—the analytic, or the search for differences—being the proper one, that synthesis should be duly combined with analysis, and that general principles should be sought as well as new forms, or so-called 'new species' and 'new genera.'* (4) It is claimed that nothing is to be gained by giving binomial names to climatic or other forms, in cases where, however considerable the differences between them may be, a complete transition from the one to the other can be traced in specimens from intermediate localities, notwithstanding the plea sometimes urged that their use affords 'convenient handles to facts.'"

No 3 of these conclusions,[5] here italicised, denotes the class of research exemplified by Dr. Ruthven's monograph. His method of approach to the problem before him is thus stated:

"Three steps are necessary to determine the genetic relationships and simplify Cope's elaborate arrangement of the group: (1) The value of

[3] *Bull. Mus. Comp. Zool.*, Vol. II, No. 3, pp. 161–450.

[4] *L. c.*, p. 163.

[5] No. 4 may be considered as an entering wedge which led up to the later adoption of trinomials. In 1872 (*Bull. Mus. Comp. Zool.*, Vol. III, No. 6, pp. 119 *et seq.*, July, 1872) varietal names were advocated and systematically adopted for intergrading forms, which were referred to as subspecies or races, the same method of designation being almost simultaneously employed by other American ornithologists and mammalogists. For several years the third term of the name was separated from the second by the interposition of the abbreviation "var.," or by a letter (Roman or Greek, according to the preference of the author); in 1877 and 1878 trinomials, pure and simple, came generally into use in this country for birds and mammals, and soon after for reptiles.

the characters must be determined; (2) geographic probabilities must be utilized; (3) similarities and intergradations must be sought."

As a result the 43 forms (20 species and 23 subspecies) recognized by Cope in his posthumous work "The Crocodilians, Lizards, and Snakes of North America" (Rep. Smiths. Inst., 1898), are reduced to nineteen; and of the twenty-two names given by Cope eighteen appear only as synonyms. Nearly seventy names have been conferred on these nineteen forms, or an average of three and a half for each.

Dr. A. E. Brown, the last preceding reviser of the group, in his "Review of the Genera and Species of American Snakes, north of Mexico," published in 1901,[6] reduced the number of forms to eighteen—ten species and eight subspecies; he proceeding on somewhat the same lines as Ruthven, namely, "that a knowledge of the laws under which forms are developed is to be best gained by a study of variations." While the number of forms admitted by the two authors is practically the same, the taxonomic results are widely diverse.

Dr. Ruthven believes that the garter-snakes will be found to furnish excellent material for experimental research, as they are hardly in captivity, and prolific; and that the first problems to be attacked are the inheritability of scale characters and the influence of inbreeding and unfavorable conditions of food and temperature. But it is to be remembered that experimental research must necessarily be conducted under unnatural conditions, and that the results do not necessarily show what has taken place under natural environments. While the results thus obtained are always interesting and suggestive, they can not be looked upon as conclusive respecting what has actually occurred under natural conditions.

J. A. A.

LEPIDOPTERA

Hybrid Lepidoptera.—Although published more than a year ago, Mr. J. W. Tutt's account of hybridization and mongrelization in Lepidoptera is probably scarcely known to evolutionists in this country. The two chapters in which he sums up and discusses all that is known on these subjects are prefaced to a much larger work, the first volume of the "Natural History of the British

[6] *Proc. Acad. Nat. Sci. Phila.*, 1901, pp. 10–110.

Alucitides." The book, a large volume of 558 pages, is part of Mr. Tutt's exhaustive "Natural History of the British Lepidoptera," this particular volume dealing with the plume moths. The treatment of the several species is even more exhaustive than that given by Mr. Scudder in his great work on the butterflies of New England; and as in Scudder's work, the purely taxonomic details are relieved by chapters on general topics.

In his two chapters, Mr. Tutt enumerates all the recorded crosses between different species (hybrids) and between different forms of the same species (mongrels), and gives numerous particulars about them. At the end of the book is an appendix describing other cases made known while the volume was in press. It appears that about 90 hybrid Lepidoptera are known, these being especially numerous among the Attacides and Anthrocerides. The well-established hybrids have been reared in captivity, and it is justly argued that many alleged hybrids found at large must be regarded with extreme suspicion, as being quite probably merely variations of one of the supposed parents. The most distantly related species which have, when crossed, produced fertile eggs and subsequent larvæ, are *Saturnia pavonia* × *Graellsia isabellæ;* but in this case the larvæ could not be raised to imagines. There is a very interesting discussion of the question whether hybridization is capable of giving rise to new species in a state of nature. This is considered extremely unlikely, for the following reasons:

"Even when hybridity is not difficult to procure between two species, the progeny shows little fertility *inter se,* and, although the males are more frequently fertile with females of either of the parent species, the female hybrids are much more rarely fertile with the males of the parent species, and at present few hybrids show comparatively free fertility *inter se.* This appears to be largely due to the anatomical and morphological upset in the sexual organs of the female hybrids, an upset that frequently finds its outward recognition in the development of gynandromorphic forms, in which the primary sexual characters are often considerably modified, and correspondingly marked changes take place in the secondary sexual characters.

"Assuming, however, hybridity ever to take place in nature, the hybrids themselves will often, presumably, follow one or other of the parent forms so far as relates to its habits, time of appearance, etc., and the chance of a male and female hybrid,

assuming that some of both sexes get through successfully, then meeting each other, as against the possibility of either meeting and pairing with or being paired with a male or female of the much more abundant parent form, is so remote that one puts aside the possibility.''

The instances of mongrelization are classified under the following headings:

1. Crossing of typical form and local race.
2. Crossing of typical form and aberration; production of artificial races by inbreeding.
3. Crossing of typical forms with aberrations tending to develop melanochroic races.
4. Crossing of typical form with aberration trying to set up local race.
5. Crossing of dimorphic forms of a species which occur together and rarely appear to attempt to supplant each other.
6. Crossing of typical forms with possible constitutional aberrations.
7. Dimorphism in one sex.

It is impossible to give any summary of the many cases described under these headings, but enough has been said to show how valuable the work is to students of evolution and variation.

T. D. A. Cockerell.

PARASITOLOGY

Parasitic Diseases in the Philippines.—The paramount importance of zooparasitic diseases in the Philippines may be judged from the recently published record of the bureau of health since the medical work at Bilibid Prison was placed under its charge in November, 1905. The prevailing diseases treated in Hospital A, Bilibid Prison, were hookworm, 1,537 cases; amebic dysentery, 551 cases; acute dysentery, 174 cases; cholera, 18 cases; pneumonia, 62 cases; beriberi, 60 cases; conjunctivitis, 221 cases, and malaria, 174 cases; 81 per cent. were thus due to animal parasites. The death rate decreased from 238 per thousand in 1905 to 13.5 per thousand in June, 1907. General sanitary measures were responsible for the first reduction to about 75 per thousand; active measures against animal parasites led to the further reduction.

The establishment of a separate department of medical zoology in the curriculum of the Philippine Islands Medical School is a natural result of the extreme prevalence of animal parasites, and of the diseases to which they give rise. About 80 per cent. of the entire population is infected, or counting different species separately, 200 infections occur to each 100 inhabitants. While the severe results of such infection noted in Porto Rico and elsewhere are not found, yet the population of the Philippines presents a higher percentage of infection with intestinal worms than has ever been definitely reported from any other people and the condition is essentially a chronic one, the results of which manifest themselves indirectly in the general physical impoverishment of the people and the high rate of morbidity and mortality accredited to other diseases.

THE PATAGONIAN FAUNA

Results of the Hamburg Magellan Expedition.[1]—The importance attaching to a knowledge of the fauna and flora of the southern extreme of South America—especially in connection with the so-called "bipolarity" theories, and with the newly explored Antarctic fauna—has been recently more fully recognized. For a long period this region was neglected. Its great distance from the centers of scientific activity, the inclement climatic conditions, the unfriendly native population, the difficulties of navigation which led every navigator to breathe more freely when he had seen the Magellanic mountains sink below the horizon in his wake—all these factors contributed to the difficulty and cost of scientific exploration, and tended to turn the scale unfavorably, when projects of collecting expeditions were discussed in Europe.

Yet the little that was known hinted of great interest in what remained to be discovered. The surveying expeditions of Fitzroy, King, Wilkes, of Nares and Coppinger, the circumnavigations of U. S. S. *Hassler* and *Albatross*, the work of the *Challenger* and of the French Mission to Cape Horn, in connection with the international polar meteorological stations—each in its turn added something to the sum total of information about these regions. The growth of commerce, with the gradual exploita-

[1] Ergebnisse der Hamburger Magelhaensischen Sammelreise, 1892–93. Herausgegeben vom Naturhistorischen Museum zu Hamburg. Bde. I–III, 1906–7.

tion of the gold-washing and sheep-raising industries of southern Patagonia, made the region more accessible; the increasing use of steam in navigation diminished the terrors of the straits for sailors, and the occasional visits of seal hunters offered opportunities for collection of other than fur animals. Really valuable material obtained for the Hamburg Museum by the merchant captains and officers Ringe, Kophamel and Paessler drew renewed attention to the subject, and projects of systematic exploration were discussed by Dr. von Neumayer and director of the museum Professor Dr. G. Pfeffer.

Times were unfavorable at first, due to civil war and other disturbances in Chile, and it was only in 1892 that it seemed prudent to actually despatch a collector.

The financial question was settled by the generosity of citizens of Hamburg and by grants from various scientific societies of the city, and plans were decided upon under the skillful direction of Dr. Pfeffer. The choice of Dr. W. Michaelsen as explorer and collector proved well advised. He left Hamburg in July, 1892, returning in September, 1893, with an extremely large, valuable and well-preserved collection in all branches; a collection believed to be the largest and most important ever brought from those shores.

Some papers on part of this collection, or partly based upon portions of it, have already appeared in various publications, notably Strebel's work on the mollusca, Michaelsen on the holosomate ascidians, Hartlaub on the hydroids, and Ohlin on the valviferous isopods.

Nearly all the various Antarctic expeditions of the last few years have touched, coming or going, on the Magellanic shores, and much of the zoological material contained in their elaborate reports has been gathered there.

Meanwhile a multitude of specialists have been busy with the Michaelsen material and many of the papers during the last ten years have been separately issued. At the present time these have been brought together, united with others not previously published, and, under the editorship of Dr. Pfeffer, issued by the Hamburg Museum in three portly, beautifully illustrated volumes.

The first volume, which relates to generalities, chordata, echinoderms and cœlenterates, has an historical preface by Neumayer, a brief account of his voyage by Michaelsen, and a

very condensed summary by the editor, in which he points out in what papers the problems of zoogeography are touched upon from the standpoint of the student of special groups, with an intimation of what will be a most welcome general discussion in the future, of those problems from a general and inclusive point of view.

The first paper is by Kustos Paul Matschie, of the Berlin Museum, describes eight species of mammals, of which one, a *Herperomys,* is described as new, and adds a catalogue of mammals of southern South America, which will be found useful, as it is annotated with mention of localities and enumeration of synonyms. As it is obviously impracticable to give within the limits of this review a synopsis of each of the multitude of papers of which these volumes are made up, the reviewer will endeavor to tabulate their contents so that those interested may find an indication of what they contain on each topic. The data on which each paper was originally separately issued are enclosed in parentheses. Each paper is separately paginated, there being no general pagination or plate numeration for the volume as a whole.

VOLUME I

* † Säugetiere. Paul Matschie (1898), pp. 30, pl. 1.
† Vögel. G. H. Martens (1900), pp. 34.
† Reptilien und Batrachier. Franz Werner (1904), pp. 21, pl. 1.
Fische. Einar Lönnberg (1907), pp. 16, pl. 1.
* Tunicaten. W. Michaelsen (1907), pp. 84, pl. 3.
* † Holothurien. H. Ludwig (1898), pp. 98, pl. 3.
* † Echinoideen. Max. Meissner (1900), pp. 18, fig. 1.
* † Crinoideen. H. Ludwig (1899), pp. 7.
* † Ophiuroideen. H. Ludwig (1899), pp. 28.
* † Asteroideen. Max. Meissner (1904), pp. 28, pl. 1.
† Alcyonarien. Walther May (1899), pp. 22, figs. 3.
† Zoantharien. Oskar Carlgren (1898), pp. 48, pl. 1.

* Paper discusses general questions, bipolarity, etc.

† Paper gives a list enumerating all the species of the region known to date.

VOLUME II—*Arthropods.*

* Hemipteren. G. Breddin (1897), pp. 38, pl. 1.
* Aphiden. H. Schouteden (1904), pp. 6.
* Formiciden. A. Forel (1904), pp. 8.
Pteromaliden. Ew. H. Rübsaamen (1902), pp. 8, pl. 1.
† * Coleopteren. H. Kolbe (1907), pp. 125, pl. 3.
* Lepidopteren. O. Staudinger (1899), pp. 118, pl. 1.

* Trichopteren. Georg Ulmer (1904), pp. 26, pl. 2.
Plecopteren. Fr. Klapálek (1904), pp. 14, figs. 10.
Ephemeriden. Georg Ulmer (1904), pp. 8, pl. 1.
* Odonaten. F. Ris (1904), pp. 44, figs. 12.
* † Apterygoten. C. Schäffer (1897), pp. 48, pl. 3.
Arachnoideen. E. Simon (1902), pp. 48.
Gonyleptiden. W. Sörensen (1902), pp. 36.
* Acariden. P. Kramer (1898), pp. 40, pl. 1.
* Pycnogoniden. J. V. Hodgson (1907), pp. 20, figs. 6.
* Myriopoden. C. Graf Attems (1897), pp. 8, figs. 4.
Schizopoden. Carl Zimmer (1907), pp. 6, figs. 17.
* Cumaceen. Carl Zimmer (1902), pp. 18, figs. 31.
* † Cirrepedien. W. Weltner (1898), pp. 16.
* † Süsswasser Ostracoden. W. Vávra (1898), pp. 26, figs. 5.
† Süsswasser Cladoceren. W. Vávra (1900), pp. 26, figs. 7.
* Süsswasser Copepoden. Al. Mrázek (1901), pp. 30, pl. 4.

VOLUME III—*Bryozoen und Würmer.*

* Bryozoen. L. Calvet (1904), pp. 46, pl. 3.
* Gephyreen. W. Fischer (1896), pp. 7.
* Hirudineen. R. Blanchard (1900), pp. 20, pl. 1.
Naiden, Tubificiden und Terricolen. F. E. Beddard (1896), pp. 64, pl. 1.
† Enchytraeiden. H. Ude (1896), pp. 44, pl. 1.
† * Terricolen (Nachtrag). W. Michaelsen (1899), pp. 28.
† * Polychaeten. E. Ehlers (1897), pp. 148, pl. 9.
† * Nemathelminthen. v. Linstow (1896), pp. 22, pl. 1.
* Chaethognathen. O. Steinhaus (1900), pp. 10.
* Nemertinen. O. Bürger (1899), pp. 14.
* Cestoden. Einar Lönnberg (1896), pp. 10, pl. 1.
Trematoden. M. Braun (1896), pp. 8, pl. 1.
Turbellarien:
  * Polycladiden. Ritter-Záhony (1907), pp. 20, figs. 9, pl. 1.
  Rhabdocoeliden und Tricladiden. L. Böhmig (1902), pp. 30, pl. 2.

The above summary is sufficient to show that these volumes form a library on the Patagonian fauna which will be indispensable to the student of the zoology of the southern hemisphere. Almost without exception the papers conclude with a full bibliography of the subject of which they treat. We hope that the concluding volume of the series which will contain the editor's general discussion will be also provided with a chart, if possible also bearing the bathymetric lines which indicate in a general way the topography of the sea bottom.

WM. H. DALL.

COLOR NOMENCLATURE FOR NATURALISTS

A Code of Colors for Naturalists.[1]—In 1905 Dr. R. M. Strong called attention in *Science* (Vol. XXI, pp. 267–268) to the availability for naturalists' use of the Bradley Educational Colored Papers. Little books containing about 165 samples of these papers may be had for five cents from dealers in kindergarten supplies. Since Ridgway's "A Nomenclature of Colors for Naturalists" went out of print, there has been no convenient and rapid means of designating colors with precision other than by the use of the Bradley papers.

The present work attempts to furnish to all who have to designate colors with precision a simple, practical and unmistakable means of indicating them. This is accomplished by supplying, at a low price, a book of convenient size for the pocket in which are contained a sufficient number of samples of different colors arranged in accordance with a recognized scientific plan and prepared with materials as durable as our knowledge of chemistry permits. All names of colors are rejected except those of the six spectral colors, red, orange, yellow, green, blue and violet. Thus is avoided the confusion inseparable from the use of names for colors. The scheme includes 24 "pure" colors, the six colors of the spectrum named above; six other colors obtained by combining the adjacent spectral colors to produce intermediate colors called red-orange, orange-yellow, yellow-green, green-blue, blue-violet and violet-red; and twelve other colors intermediate between the twelve above named. Thus between red and red-orange there intervenes a lighter red, between red-orange and orange a lighter red-orange, so that the order of the twenty-four colors is as follows: red, red, red-orange, red-orange, orange, orange, orange-yellow, orange-yellow, yellow, yellow, etc. Each color is intermediate between that which precedes and that which follows it. Each of the twenty-four pure colors is made the basis of a double page of samples, on which it appears along with twenty-nine tints, shades and broken colors produced by mixing the pure color with white, black or gray. Twenty-four of these tints and shades and broken colors, in which the white and black are

[1] Klincksieck, Paul, et Valette, Th. Code des Couleurs à l'usage des Naturalistes, Artistes, Commerçants et Industriels, 720 Échantillons de Couleurs classés d'après la méthode Chevreul simplifiée. Paris, 1908; 1 vol., 86 pp., 4¾ x 7½ in. 48 pages contain 720 samples of colors.

used in definite proportions, are numbered consecutively with the pure color from which they are derived, so that the first double page of samples contains reds numbered from 1 to 25, the second reds numbered from 26 to 50, the third red-oranges from 51 to 75, the fourth red-oranges from 76 to 100. Thus the first 100 numbers are given up to red (including red-orange), the numbers from 101 to 200 indicate oranges (including orange-yellow), and so on through the spectrum, until the numbers 501 to 600 indicate violet (including violet-red). In addition to the six hundred colors thus numbered consecutively, there are 120 others, five on each page, all made by adding white to the pure color or to one of the broken colors and all designated by prefixing letters to the numbers on the same page. Thus the number of colors is brought up to 720.

To designate a color it is only necessary to refer to it by its code number. Thus a naturalist may describe the color of a bird as C. C. 120 (C. C. as an abbreviation for Code des Couleurs), and one reading his description knows at once, since the number falls in the second hundred, that the color is a broken orange and by turning to his code has the color itself before him. The naturalist may carry the book into the field and on a pencil sketch may enter the numbers of the colors of natural objects, and from such notes may, at his leisure, prepare colored figures of such objects, long after the objects themselves have faded. Thus there is provided an international code of colors which may be used like a telegraphic code and by means of which men of different nations and professions may intercommunicate without risk of being misunderstood.

The scheme adopted in the code is a simplification of that used in the dye works at Gobelin and elaborated by the chemist Chevréul formerly in charge of the dye works. The simplification consists in reducing the number of pure colors from 72 to 24, in greatly reducing the number of tints and shades and broken colors, and in omitting the grays. The omission of the grays is justified on the ground that all grays are in nature impure, and are therefore represented in the "Code" by shades or broken colors. The Chevréul scheme contains 14,421 colors. including grays, while the "Code" contains but 720, excluding grays. The colors given in the "Code" are, however, so close together that only the trained expert will be able to discriminate intermediate colors; they are probably sufficient for all practical

purposes. They are between 4 and 5 times as many as in the Bradley papers, which have also been arranged in accordance with the scheme of Chevréul (Milton Bradley, Elementary Color).

M. Th. Valette, chemist of the government tapestry works at Gobelin, has selected the pigments used with special reference to their durability. The pigments have been applied to paper without the use of oil as a vehicle, so that their durability is thereby increased. The colored paper has been coated with an insoluble gelatin to protect it from the action of water. The paper thus prepared has been cut into samples 20 by 25 mm., and these have been pasted to the pages of the "Code." The book, thus prepared, seems to answer the needs of naturalists far better than any other practicable scheme, and its use should greatly lessen the growing confusion which has resulted from attempts to designate colors by names without any standard of reference. The writer has tested the book in the field with satisfactory results. While not all colors may be matched by it, the results are accurate enough for practical uses, and greater accuracy is at present to be had only by the use of the color wheel.

JACOB REIGHARD.

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THE AMERICAN NATURALIST

A MONTHLY JOURNAL
DEVOTED TO THE NATURAL SCIENCES
IN THEIR WIDEST SENSE

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THE

AMERICAN NATURALIST

Vol. XLII — *September, 1908* — No. 501

SOME RESULTS OF THE FLORISSANT EXPEDITION OF 1908

PROFESSOR T. D. A. COCKERELL

University of Colorado

The fourth University of Colorado Expedition to Florissant, in the summer of 1908, was only about three weeks in the field. The earlier expeditions, in 1905, 1906 and 1907, obtained a very large amount of material from the Miocene shales of this locality, and much of this still awaits study and description. A general account of Florissant appeared in the *Popular Science Monthly* for August, 1908, while briefer statements, more or less inaccurate, may be found in the current geological textbooks;[1] so it will not be necessary at this time to give a description of the place or the fossil-beds. It is pro-

[1] In Dr. W. B. Scott's valuable "Introduction to Geology," 2d ed. (1907), p. 756, it is stated that there were "very few palms." As a matter of fact, there is no reason for believing that there were any. The Rhus sp. on p. 755 is *Weinmannia phenacophylla* Ckll. In Vol. III (1906) of "Geology," by Professors Chamberlin and Salisbury, Florissant is referred to the Oligocene, following Scudder and others. It is stated that "palms are barely represented," and yews are said to occur. We do not know of any yews. It is also stated that over 700 species of Florissant insects were described by Scudder; the actual number is 569. In Handlirsch's admirable work "Die Fossilen Insekten," which would naturally be regarded as representing the best modern knowledge, numerous identifications of Tertiary insects are cited, which certainly have no value. Thus Scudder had a specimen for Florissant which looked like a Bombus: this appears in the list, without any query, as Bombus. I have seen the specimen, and it is not a bee. In Dr. Folsom's "Entomology" (1906) masses of Sialid eggs are said to occur; the eggs in question were not from Florissant, but from the Laramie beds at Crow Creek.

posed, instead, to call attention to a few of the most interesting finds of this year, especially those which can readily be illustrated by photographs. Most of the work this year was done at what we call Station 13 B, close to, and apparently of the same materials as, Station 14, from which the best things of former years have nearly all come. Superficially, 13 B seems to dip under 14, but this appears to be due to a fault; both beds belong to the older series of the locality, being covered by extensive deposits of rock and shale, the greater part of which, at 13 B, has been removed by erosion.

The shale at 13 B proved extremely uneven in quality. During the first week the results were perhaps better than in any week of former years; but the last two weeks were relatively barren, and, as we were getting a large proportion of duplicates, it was doubtful whether the work justified the expenditure. It is highly important, of course, that the Florissant beds should be further explored, and no doubt the treasures yet to be uncovered there are innumerable; but with limited resources, and great accumulations of unworked materials on hand, it has seemed better not to continue digging at the present time.

At the University of Colorado an exhibit of the Florissant fossils has been arranged. It is probably the best in existence, although the insect specimens in the Scudder collection at the Museum of Comparative Zoology, none of which are on exhibition, far exceed ours in number and variety. From the recently gathered materials, a series will be prepared for Colorado College, and also one to be sent to Dr. R. F. Scharff, for the Dublin Museum.

The members of the 1903 expedition were the same as in 1907, with the addition of Mr. Melford Smith, and, for a shorter time, Miss Gertrude Darling.

The Fish-genus Trichophanes

In 1872 Cope published Trichophanes, a new genus of Perciform fishes, represented by a small specimen obtained in the coal shales north of Osino, Nevada. In 1878

two other species, *T. foliarum* Cope, and *T. copei* Osborn, Scott and Speir, were added from the Florissant shales. *T. copei,* which has not been figured, is stated to differ from *T. foliarum* by its smaller scales. The genus is one of quite unusual interest, because it appears to belong to the suborder Xenarchi, an old group with peculiar anatomical characters, represented to-day by a single species, *Aphredoderus sayanus,* confined to the eastern United States. According to Jordan and Evermann, the Xenarchi are related to the Percopsidæ, of which two liv-

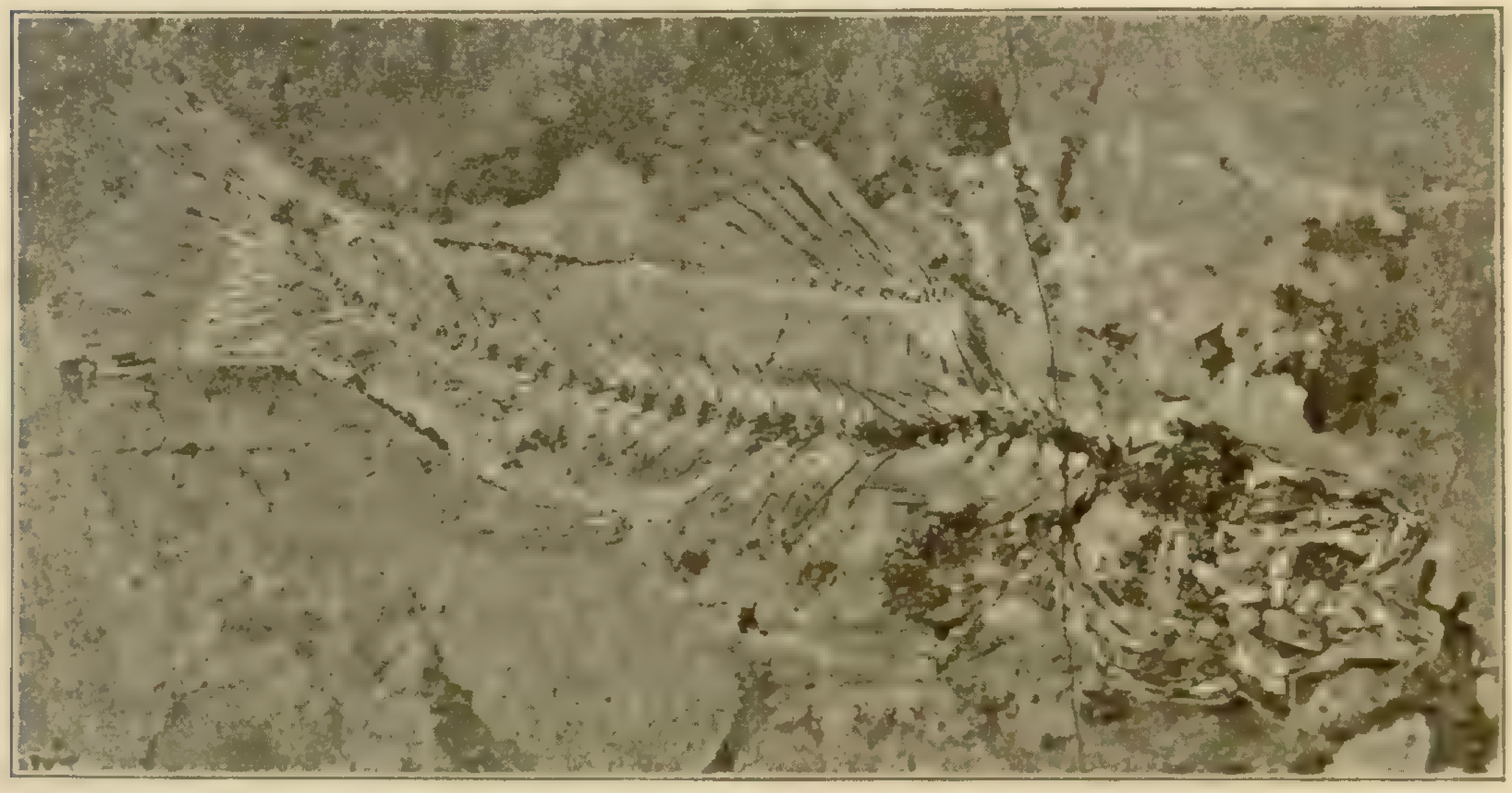

FIG. 1. *Trichophanes foliarum* Cope.

ing species are known—*Percopis guttatus* Agassiz, from the Great Lakes and surrounding regions, and *Columbia transmontana* Eigenmann, from the Columbia River. These fishes are evidently remnants of an ancient fauna, which in Tertiary times included a variety of genera and species. Agassiz, when describing Percopsis, was much impressed by its generalized features, combining characters which commonly existed together in Cretaceous fishes, but are widely separated in modern forms. "Now my new genus Percopsis is just intermediate between the Ctenoids and Cycloids; it is what an ichthyologist at present would scarcely think possible, a true intermediate type between Percoids and Salmonidæ" (Agassiz, 1850). It is remarkable that this relic of earlier days should now

have its headquarters in the area which was covered by the glacial ice; it is possible, perhaps, that it lived through the glacial period in some northern locality which was unglaciated, but cut off from the southern fauna. In this way, it might have been protected from the stress of competition, and when the great lakes were opened up, it found in them a comparatively free field—a field apparently not yet populated with anything like the maximum number of species.

FIG. 2. *Trichophanes foliarum* Cope.

Trichophanes is not precisely typical of Aphredoderidæ; it certainly seems to have some characters resembling those of the Percopsidæ, no doubt indicative of real relationship. It is readily recognized by its peculiar scales, which are ultra-ctenoid, with the marginal teeth produced into quite long bristle-like structures. According to Cope, they are "without or with very minute sculpture," but under the compound microscope they are seen to be covered with fine concentric striæ.

Cope's type of *Trichophanes foliarum* was obtained by Dr. Scudder, and consists of the anterior half of the fish only. This year my wife found at Station 13 B two prac-

tically complete specimens, herewith illustrated. These reveal many characters not visible in the type, and emphasize the Percopsis-like tendencies. In Jordan and Evermann's "Fishes of North and Middle America," plates CXXI and CXXII, are given excellent figures of Percopsis, Columbia and Aphredoderus. Our Trichophanes agrees with Aphredoderus in the thick (deep) caudal peduncle, the projecting lower jaw, and the scaly sides of the head. The dorsal fin, as in Aphredoderus, has three spines, the first very short, the third long (about 12.5 mm.), the second intermediate. The anal, as in

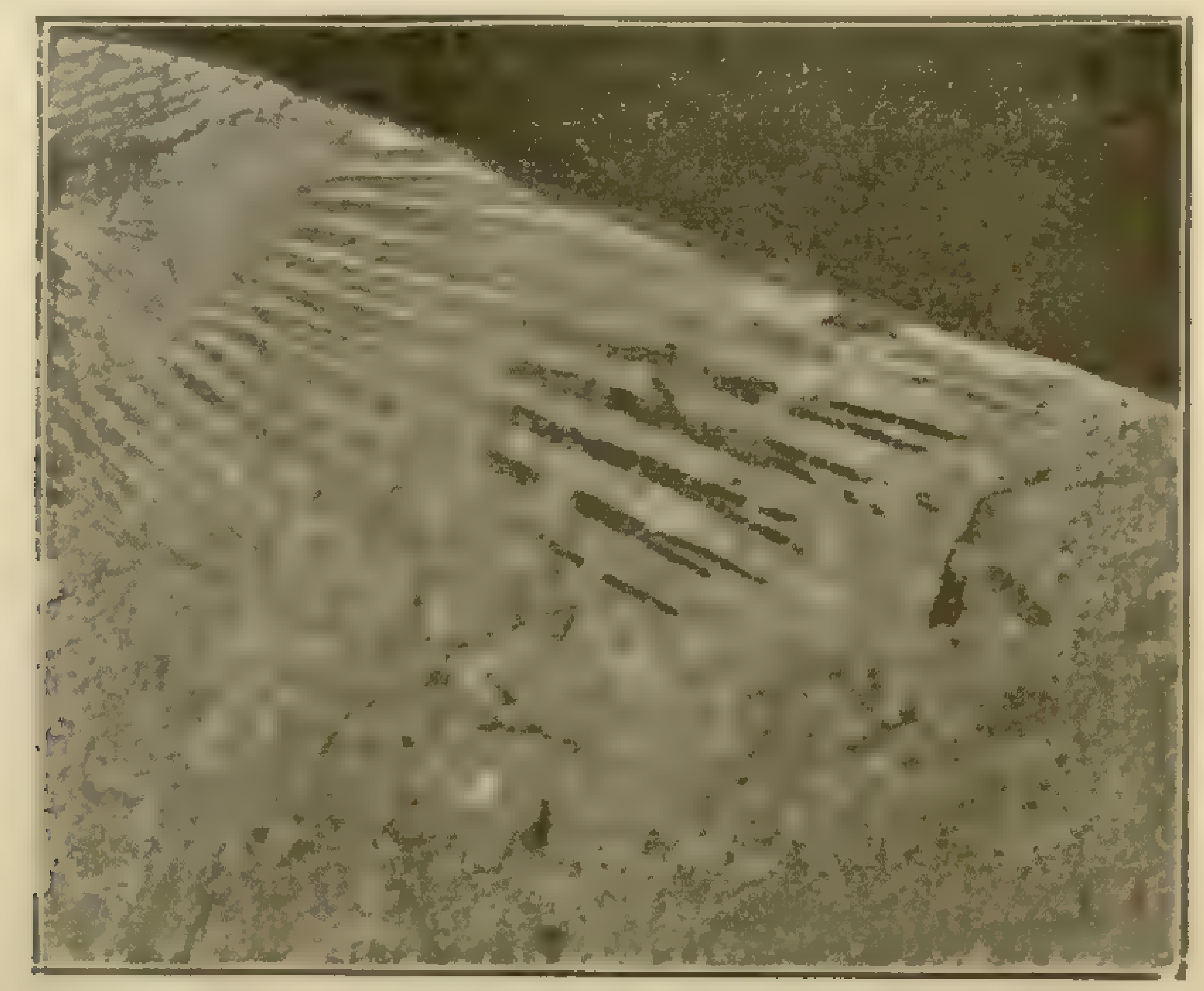

Fig. 3. Caudal fin of Amia.

Aphredoderus and Columbia, but not as in Percopsis, has two spines, one long, the other short; the longer spine is nearly straight, as in Aphredoderus. The shape of the dorsal is very much like that of Percopsis, not very like that of Aphredoderus; while the forked caudal is very unlike that of the latter genus, but rather closely resembles that of Columbia. There is no adipose fin (it is present in Percopsidæ); the ventrals are inserted about 5 mm. posterior to the bases of the pectorals, and the same distance anterior to the level of the beginning of the dorsal. In the last character the fish is nearly intermediate between Aphredoderus and the Percopsidæ.

Trichophanes should apparently be taken as typical of a family Trichophanidæ, falling in the Xenarchi, and

standing between Columbia and Aphredoderus in the serial arrangement.

Another waning group of fishes (with a single living species) found at Florissant is Amia, the bowfins. The accompanying figure shows a tail of this genus we found; much hunting failed to discover the rest of the specimen.

A PRIMITIVE DRAGONFLY

The Zygopterous dragonflies are divided into families known as Calopterygidæ and Agrionidæ. The Calopterygidæ are further divided into subfamilies, separable

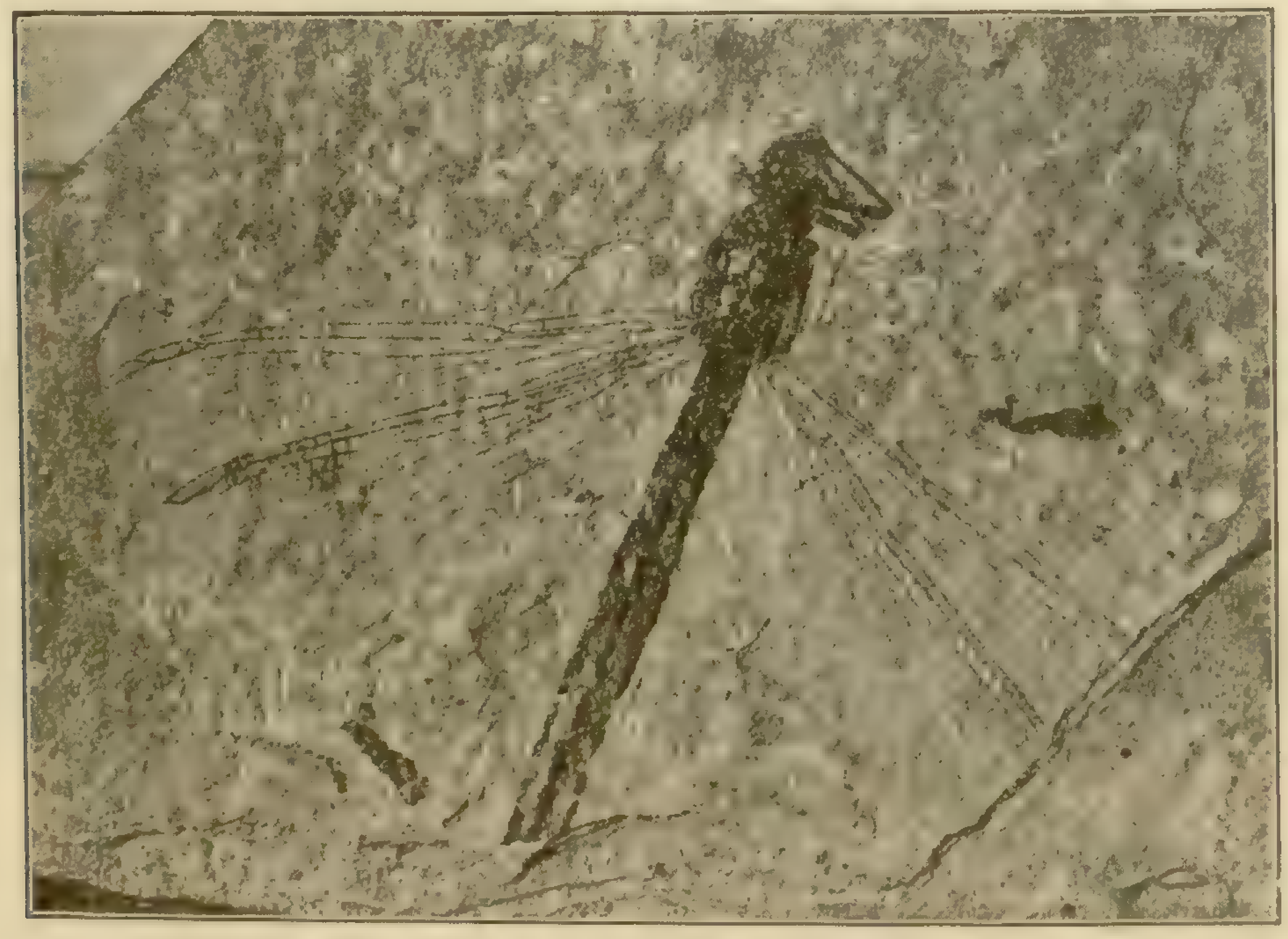

FIG. 4. *Phenacolestes parallelus* Ckll.

by the character of the costal region toward the base of the wing. In the Calopteryginæ, this area, before the nodus, is crossed by four or more veins, called antenodals; in the other subfamily, the Lestinæ, these have been reduced to two. In the family Agrionidæ, which is very abundant in the modern fauna, the reduction to two antenodals is practically universal. There is, however, an extinct subfamily, which I have called Dysagrioninæ, in which this reduction has not gone so far, and four or more antenodals remain. Of this group we know two genera, Dysagrion Scudd, from the Green River beds, and Phenacolestes Ckll. from Florissant. The latter genus,

published early in 1908 (*Bull. Amer. Mus. Nat. Hist.*) was known only from the wings. A photograph of a wing was sent to Dr. Needham, who wrote: " It is indeed a most interesting fossil, another synthetic type. . . . De Selys' Podagrion group of Agrioninæ includes the most primitive members of that subfamily, and this fossil is more primitive in several characters than any living forms." Very fortunately, a splendid specimen of *Phenacolestes parallelus* was uncovered this year by Mr. Geo. N. Rohwer. As the illustration shows, it is nearly complete, lacking, however, the apex of the abdomen. The wings are not so heavily clouded as in *P. mirandus,* the type of the genus, and there are differences in the venation. *P. parallelus* was originally described from the apical half of a wing.

Some Fossil Bees

In 1906 (*Bull. Mus. Comp. Zool.*) I described a bee's wing found at Florissant by Scudder, regarding it as the type of a new Anthophorid genus, Calyptapis. A very

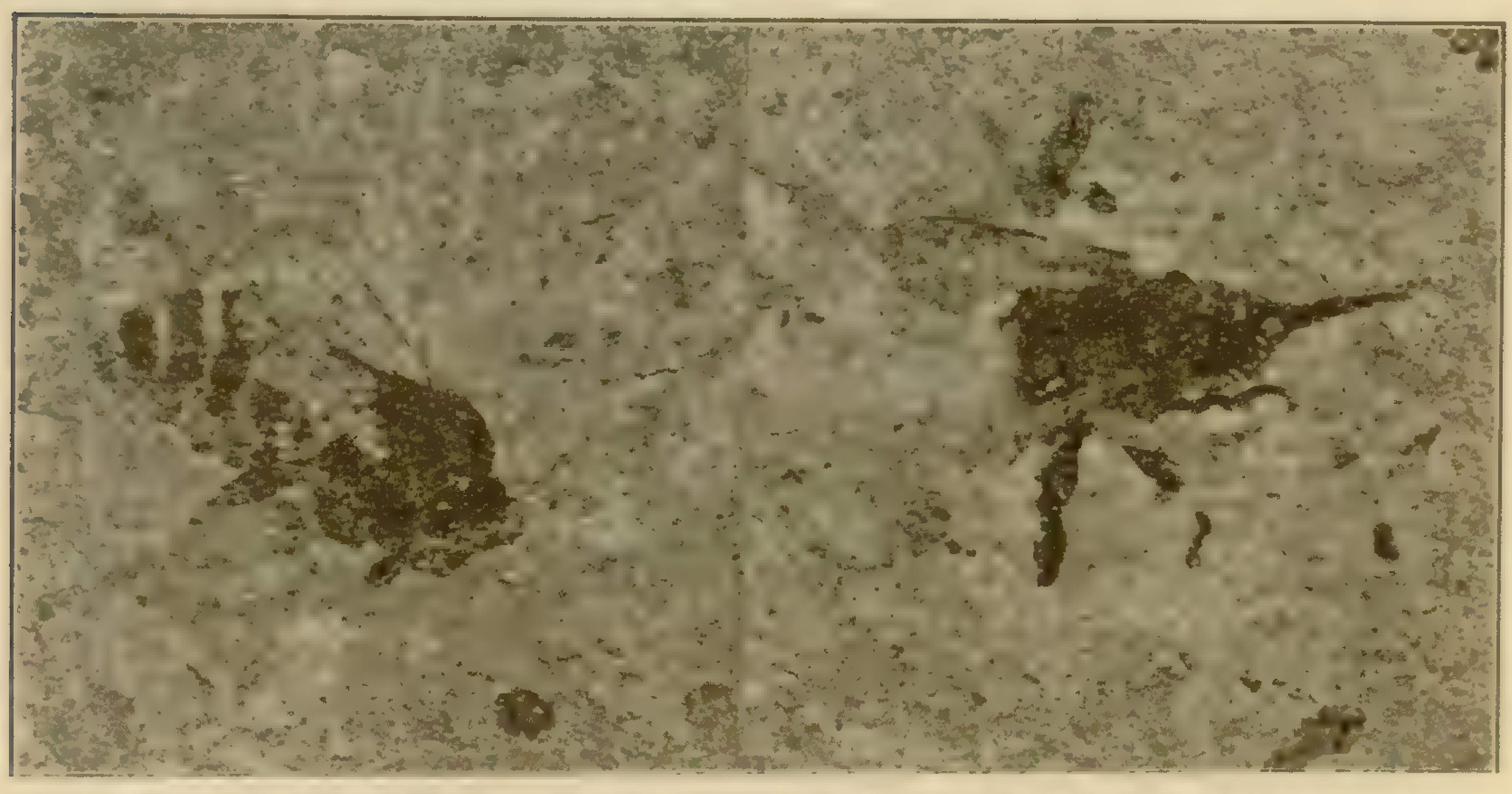

Fig. 5. Fossil bee, *Calyptapis florissantensis* Ckll.

Fig. 6. Fossil bee, *Anthophora melfordi* Ckll.

fine example, showing the body, was found this year, and from a close examination I am able to ascertain its true position. It is not an Anthophorid at all, but is a genus of Bombidæ, in other words a bumble-bee. The genus is valid, and gives the first indication of the former history

of this group in America. The insect was especially interesting to me, because I had just been studying the bees in Baltic Amber, which include various genera and species of still earlier bees related to Bombus.

Another bee of great interest was a species of Anthophora, with the mouth-parts exserted and plainly visible. Some of the amber bees show the mouth-parts very well, but it is extremely rare for those in shale to show anything of the kind. The genus Anthophora is common in Colorado to-day, but it was not previously known from the American Tertiaries.

A Problematical Flower

Last year we found, among other flowers, one which was so interesting, and so well preserved, that Dr. Arthur Hollick made it the subject of a special article in *Torreya*, September, 1907. Dr. Hollick named it *Phenanthera petalifera*, new genus and species, but was unable to place

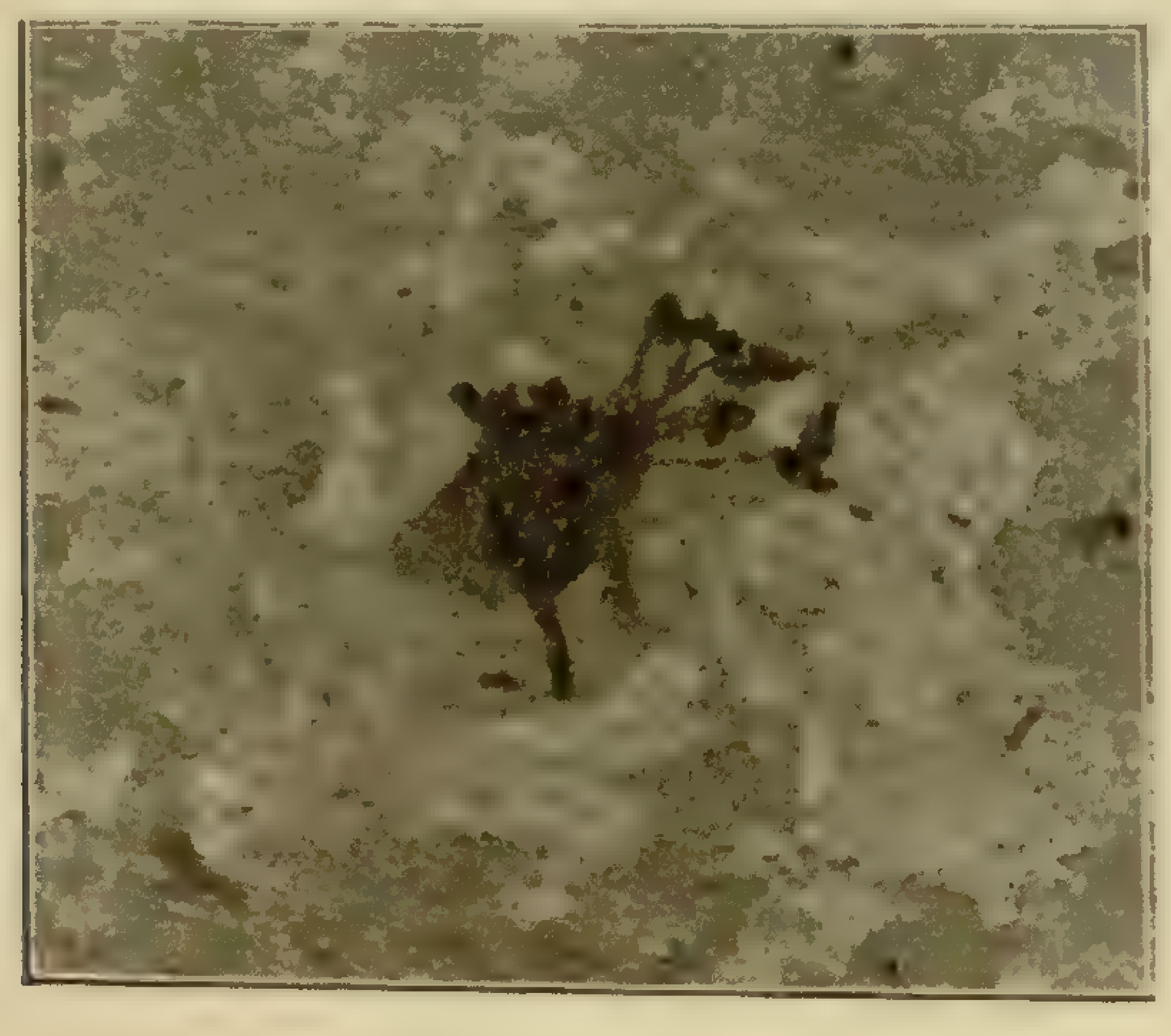

FIG. 7. Fossil flower, *Phenanthera petalifera* Hollick.

it definitely in any known family. A new specimen, figured herewith, is clearly of the same species, and on the whole confirms Dr. Hollick's description. The stamens, with long filaments and large anthers, are certainly eight in number. The supposed appendages of the calyx seem to me to be emarginate, and to resemble rather closely the small petals of certain *Ribes*. Following this clue, the large, thin "petals" may be interpreted as petaloid calyx-lobes, also as in Ribes. The short pedicels, about the length of the hypanthium, suggest that

the flowers were borne in clusters, and so in all respects they seem to agree sufficiently with Ribes, except for the insuperable difficulty of the eight stamens. The eight stamens would agree with Weinmannia, but the flower otherwise seems discordant, judging from the descriptions—I have never seen a Weinmannia flower. Both Weinmannia and Ribes are represented by leaves in the shale.

The Problem of the Proteaceæ

The Proteaceæ constitute a rather large and very characteristic family, with over 950 living species, almost confined to the Southern Hemisphere. Nearly 600 are Australian; New Caledonia has 27, New Zealand 2, Chile 7, tropical South America 36, South Africa over 250, Madagascar 2, and the mountains of tropical Africa about 5. These particulars are taken from Engler (1894), probably the numbers should now be somewhat increased. The genus Helicia, with some 25 species, is Indo-Malayan, and extends north of the equator as far as the Himalayas.

One of the most remarkable discoveries—if such it be—of paleobotany is that of the occurrence of Proteaceæ in abundance in the Tertiaries of the Northern Hemisphere. In Ettinghausen's work on the fossil flora of Häring (1853) numerous remains of leaves are figured, together with drawings of recent species of Proteaceæ. The resemblances are not merely close; it is not too much to say that the oligocene leaves look practically identical with their modern representatives. Furthermore the resemblances are not shown in one or two types only, but extend throughout a considerable series; nor are they confined to the leaves—the determinations in some instances are fortified by characteristic-looking seeds. Even the peculiar fruits of Persoonia are shown. Such evidence looked convincing enough to Ettinghausen, and *a priori*, there seemed to be no obstacle. The distribution of the Proteaceæ to-day seemed to be that of a group once world-wide, but now driven to the ends of the earth by the stress of competition. This would agree well with

the case of the marsupial mammalia, and others such as the recently elucidated one of the Chrysochloridæ, or golden moles.

On the other hand, it was pointed out that there were other leaves resembling those of the Proteaceæ. In 1870 Bentham went so far as to say, in regard to detached leaves, "I do not know of a single one which, in outline or venation, is exclusively characteristic of the order, or of any one of the genera." Quite recently Dr. Schönland (*Trans. S. African Phil. Soc.,* 1907, p. 321) has written: "The supposed identifications of southern types of plants in the Tertiary deposits of the Northern Hemisphere are considered by most eminent botanists, such as Sir Jos. Hooker, the late Mr. G. Bentham, A. Schenk, etc., as worthless. Laurent has recently tried again to prove that the Proteaceæ originated in the North, but the evidence on which he relies seems to be altogether untrustworthy." Without having seen the European fossils, it may be hazardous to attempt any contribution to this controversy; but it must be pointed out that those who regard the paleontological evidence with contempt seem to have forgotten one or two things. They have not sufficiently remembered the great antiquity of the genera of flowering plants, as shown by indisputable evidence; they have failed to consider the great lapse of time, which would permit migrations from one end of the world to the other (continuous land provided), even at the slowest rate; and more especially, they seem to have forgotten the unquestioned cases of Sequoia, Comptonia, Liquidambar, etc., in which wide-spread types have been reduced to comparatively small areas within quite recent geological times. It may also be added, that they have overlooked the analogous cases among animals, which can by no means be explained away. With all this, it must be confessed that the dicta of paleobotany are not so reliable as we could wish, and that an attitude of scepticism is often more than justified.

Lesquereux believed that he could recognize a considerable series (8 species) of Proteaceæ in the Florissant

shales. They are by no means so convincing as the European fossils; but they appear to represent an element now wanting in the North American flora, and no one has been able to show that they are *not* Proteaceous. I give figures of two of the most characteristic—*Lomatia acutiloba* and *Lomatia tripartita*. Our new material of *L. tripartita* is especially interesting as showing—what Lesquereux did not know—that it has compound leaves.

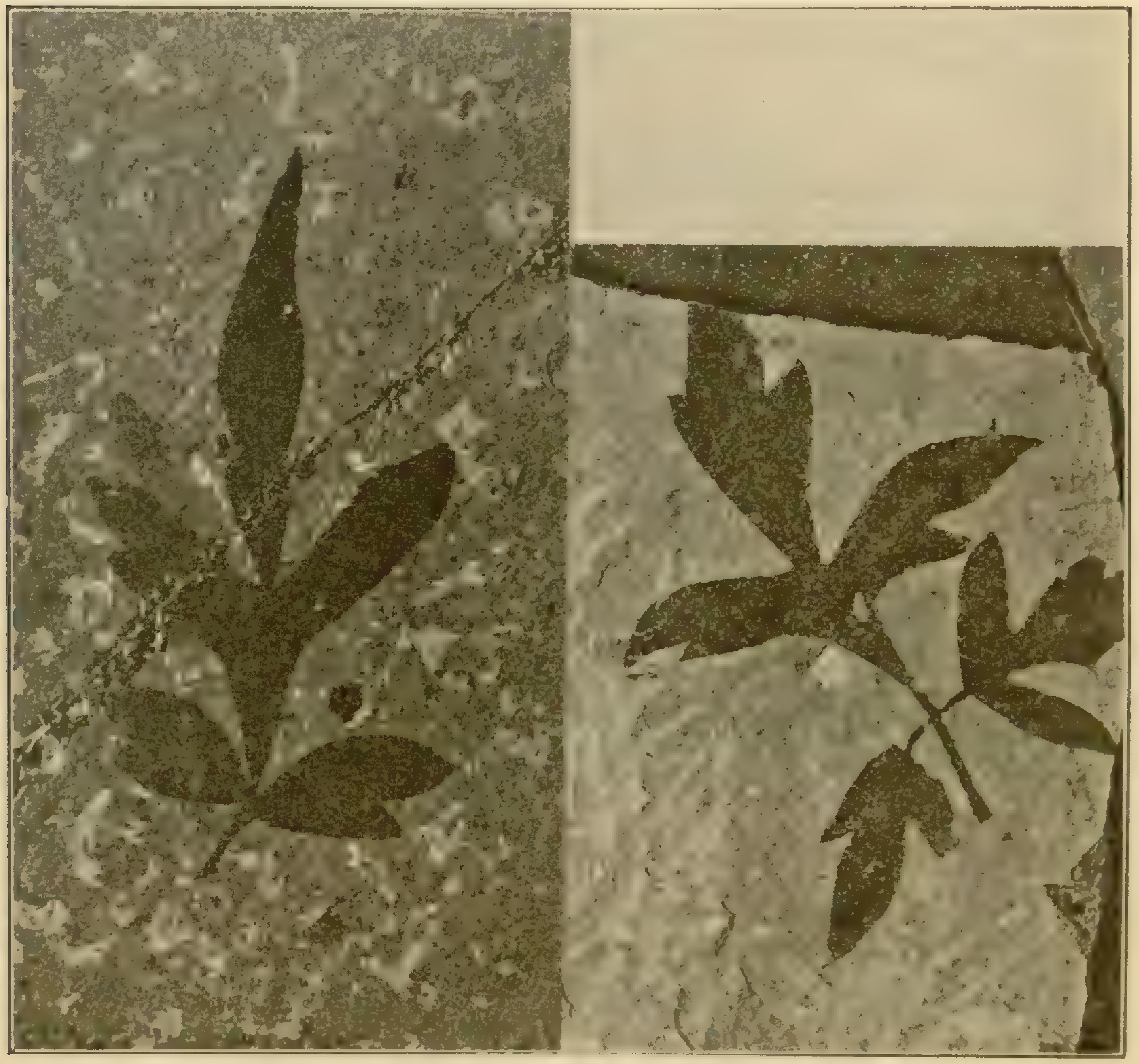

Fig. 8. *Lomatia tripartita* Lx. Fig. 9. *Lomatia tripartita* Lx.

These leaves are exceedingly variable, and have very much the cut of certain species of Phacelia.

This question of the Proteaceæ is one of wide importance, for it is not only a test of the accuracy of paleobotanical conclusions, but, according as it decided one way or the other, it provides or removes an argument for the former existence of great southern lands between the present continents.

A Fossil Milkweed

On the same piece of shale as the *Lomatia acutiloba*, found by Mr. S. A. Rohwer at Station 20, is the follicle of a species of milkweed. It is 54 mm. long, 14 wide in the middle, dark colored as preserved, with a longitudinal suture and without tubercles. It closely resembles the follicle of the modern *Acerates auriculata*, but is rather less tapering. It may be known as *Acerates fructifer*, n. sp. A similar follicle was described by Heer as *Acerates veterana*, and was found at Œningen and other localities.

Fig. 10. *Lomatia acutiloba* Lx., and follicle of *Acerates fructifer* n. sp.

A Serviceberry

I give a figure of large serviceberry leaf, *Amelanchier typica* of Lesquereux. It is like that of the modern American *A. canadensis*, but the more cuneate base resembles that of *A. intermedia*. Other species of Amelanchier have been found at Florissant, all having a completely modern appearance, and showing that the minor groups of the genus were separated in the miocene.

A Prickly Araliaceous Plant

At Station 13 B Mr. S. A. Rohwer found a leaf with five oblong, long-stalked leaflets, as preserved light red-

dish in color, with the petiolules provided with small but very distinct recurved prickles. The leaflets are about 48 mm. long and 24 broad, with a cordate base, and the margin with broad rounded teeth or pronounced crenations, each about 2.25 mm. long. The principal lateral veins, leaving the midrib at an angle of perhaps 50°, are about seven in number on each side, and are only moderately curved. The petiolules differ greatly in length, from 26 to 5 mm., and bear a moderate number of irregularly-placed prickles, these being about 2 mm. long.

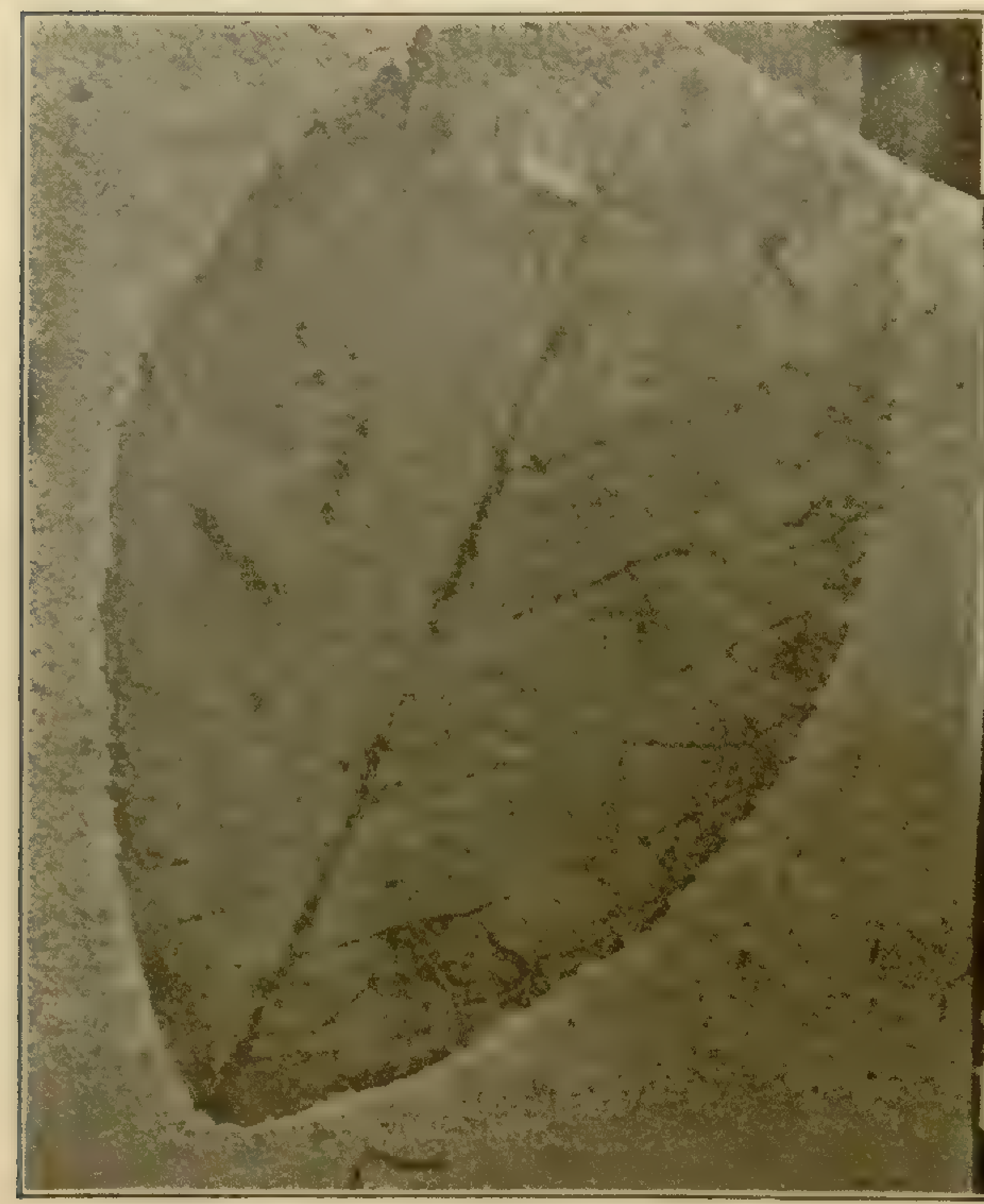

FIG. 11. Serviceberry leaf, *Amelanchier typica* Lx.

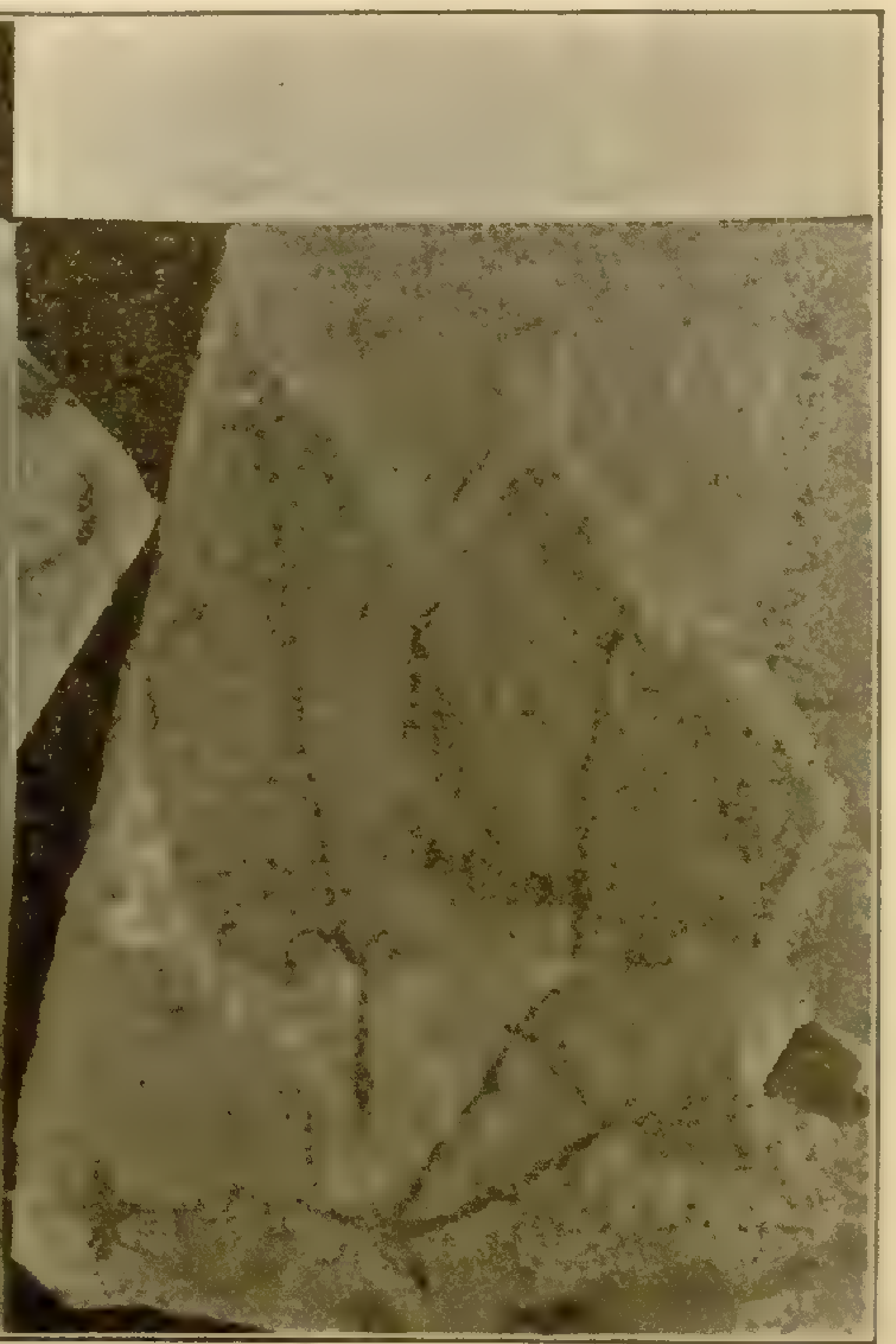

FIG. 12. *Panax andrewsii* n. sp.

Mr. D. M. Andrews, of Boulder, suggested to me that this fossil was Araliaceous, and upon looking the matter up, I felt satisfied that this must be correct. I sent a photograph to Dr. N. L. Britton, who kindly replied: "There is no doubt that the photograph that you send represents some species of Araliaceæ, but I am not personally acquainted with anything quite like it. A good many of the woody Araliaceæ have prickles." From the leaf alone, the restricted genus must remain somewhat doubtful, but it may be permissible to refer the plant to *Panax*, under the name *Panax andrewsii* n. sp.

EMBRYOLOGY OF MYOSURUS MINIMUS

LEROY D. SWINGLE, Ph.D.
University of Nebraska

There is a close superficial resemblance existing between Myosurus and some of the lower forms such as the pines and the Selaginellaceae. For this reason the development of Myosurus presented itself as an inviting field of research. To be sure Bessey (1898) has already given the stages in the development of the pistils. My work in so far as it repeats these early stages serves as a confirmation of his description.

The developmental stages correspond very closely to those of Ranunculus, which has been investigated by Coulter (1898). The arrangement of the pistils, however, differs from that of Ranunculus in the fact that in Myosurus the receptacle is drawn out into a long central axis around which the pistils are arranged in spiral rows. Acropetal development of the pistils is very marked, so that the axis may lengthen nearly two inches after the pistils at the base have reached maturity (Pl. I, Fig. 8). The pistils formed late in the season around the apex of the axis are not pollinated. In respect to this conical arrangement of megasporophylls and the mode of development of the megasporangia there is at least a superficial resemblance to the pines and Selaginella.

As in most microsporophylls, so here there are four sporangia. At first the stamen is a mass of undifferentiated meristem (Pl. I, Fig. 1), but soon the limits of the sporangia become visible. The meristem cells within the areas which are to become sporangia begin to degenerate, while the first hypodermal layer becomes active in division. The cells, archesporial in character, divide periclinally to produce an outer primary wall cell and an inner primary tapetal cell. The former cell divides once

or twice, producing three or four layers in the wall. The latter cuts off spore mother cells which take the place of the degenerating meristem. The tapetal layer appears to be the outer layer of spore mother cells which have sacrificed their reproductive function for the nourishment of the other cells (Pl. I, Fig. 2). In this earliest stage of tapetal differentiation, some of the tapetal cells are binucleate. A little later practically all of them become binucleate and remain so till degeneration is accomplished (Pl. I, Fig. 3). This fact, to my mind, supports the theory that tapetal cells are potentially spore mother cells. The hereditary stimulus toward further division to form microspores is strong enough in them to carry the nucleus through one division, at which point their new function usurps control and arrests further development.

The mother spores are few in number and as the anther enlarges become rounded off and separated from each other (Pl. I, Fig. 3). The usual course of development now follows. The mother cells divide simultaneously in a given sporangium to form first two and then four cells arranged either tetrahedrally or in the same plane (Pl. I, Fig. 4). The last three stages in the maturity of the microspores are shown in Figs. 5, 6 and 7. There are developed on the wall three thin spots for the extrusion of the tube. The tube nucleus, the round one, and the generative nucleus, the oval one, are always present before the pollen leaves the anther. Upon germination the generative nucleus evidently divides, for two male nuclei are found in the pollen tubes. Degeneration of the tapetum is not very marked till the pollen grains are completely formed. In the mature anther not only the tapetum but all the other cells of the wall except the epidermis and first hypodermal layer have disappeared. This hypodermal layer develops heavy bands in the cell walls for breaking the anther.

The pistil appears in its earliest stage as a small swelling on the side of the receptacle (Pl. I, Figs. 8–9).

Soon this mass of cells bends a trifle downwards, and the anlage of the sporangium appears as a swelling in the distal axil formed by the juncture of the sporophyll with the receptacle (Pl. I, Figs. 8 and 10). The end of the sporophyll now begins to bend upwards and the ovule downwards. About this time the archesporial cell appears as a single large hypodermal cell (Pl. I, Fig. 13). When the ovule has bent downwards about 90° and the seed coats have begun to appear at its sides as slight elevations, the archesporium divides rapidly to form four megaspores, arranged approximately in a longitudinal row. The first two, however, often lie more or less side by side (Pl. I, Fig. 11). In a few cases I found only three megaspores. This may have been because of tardiness in the division of one of the cells. Meanwhile a groove has been forming in the upper surface of the carpel, and as the carpel continues to bend upwards the ovule is entirely enclosed by the sides and bottom of the groove. By the time the megaspores are formed, the upper convex surface of the ovule has fused with that portion of the pistil next to it. The ovule now hangs loosely downwards in the cavity thus formed. The nucellus continues its circular movement and by the time it has bent 180° the megaspore next to the chalaza, the functional one, has enlarged, while the others have begun to degenerate. When the ovule has described an arc of 225° the functional megaspore has made its first division. Between the two nuclei a large vacuole, which continues to enlarge with the growing sac, is formed (Pl. I, Fig. 12). The cells at the sides of the sac crowd in between the sac and the epidermis. At this stage the seed coats are prominent and have three or four layers of cells. In the next stage the nucellus has advanced about 90° farther in its cycle and each nucleus of the sac has divided. With the increase in size of the sac, the cells round about it begin to degenerate. The seed coats are now as long as the nucellus (Pl. II, Fig. 14). While the nucellus is passing through the next 45° of arc all the nuclei of the

sac divide, forming eight nuclei, four at each end of the sac. The nucellus now lies parallel to the axis of the receptacle with the micropyle, which is now completely formed, directed upwards (Pl. II, Fig. 15). One nucleus from each end of the sac moves toward the center where they fuse to form the definitive endosperm nucleus (Pl. II, Fig. 17). At first this nucleus is characterized by two nucleoli (Pl. II, Fig. 19), the others having only one. Maturation is now complete, and the cell which is to become the functional egg cell may lie between or at either side of the synergids.

The pistil has now reached its final stage. It makes a slight angle with the receptacle (Pl. II, Fig. 15). The stigmatic surface is marked by long spreading cells (Pl. II, Fig. 16). The presence of chloroplasts in the cells of the style and epidermis will be noted. The ovarian cavity is almost entirely filled with the ovule. It is lined with a layer of cells which represent the original epidermal layer before enclosure took place. In surface view they are seen to be irregular cells with wavy walls (Pl. II, Fig. 24). Immediately underneath this layer is one, or in some places two, layers of long interlacing cells formed from the fibro-vascular bundle. They form a firm basket-like structure.

Already, even before the definitive endosperm nucleus is formed, the pollen tubes are found in the micropyle. About the time of the formation of the endosperm nucleus the pollen tube enters the sac (Pl. II, Figs. 18–19). The synergids at once begin to degenerate. As the tube passes into the sac the egg nucleus and the endosperm nucleus move towards each other (Pl. II, Fig. 19). The cytoplasm around the egg nucleus becomes denser and soon distinct from the other cytoplasm. It is not certain about the conduct of the generative nuclei, actual fusion stages not having been observed. Except for a few isolated observations the evidence points to the fact that the endosperm nucleus is fertilized by one of the generative nuclei and the egg nucleus by the other. The isolated

observations just mentioned were to the effect that both male nuclei were present in the sac after the endosperm nucleus had proceeded to divide. At any rate, whether the endosperm nucleus requires fertilization or not, it precedes the egg nucleus in division. This fact supports the theory that the endosperm is a portion of the gametophyte.

The first division of the egg cell is periclinal, forming two cells, the distal one of which is destined to give rise to the embryo and the other the suspensor. These two cells then divide almost simultaneously, the former transversely, lengthening the suspensor, the latter longitudinally. Either may, however, precede the other in dividing. The four-celled stage is formed by a division of the two cells in a longitudinal plane at right angles to the first plane. One or both, generally one, of the cells of the suspensor divides transversely, thus completing the suspensor which possesses three or four cells (Pl. II, Fig. 20). The proximal cell often broadens at its base. The next division of the embryo cells is at right angles to the other two planes of division and results in an eight-celled stage (Fig. 20). About this time the distal cell of the suspensor makes two longitudinal divisions at right angles to each other (Pl. II, Figs. 21–22). Numerous divisions follow in the usual manner (Figs. 21–22). In the last stages the exact arrangement of cells was hard to determine on account of the difficulty in sectioning the hardened wall of the sac. But the shape of the mature embryo with its two cotyledons and the approximate arrangement of cells are shown in Fig. 23. The embryo lies in a cavity about twice its size and so does not come into contact with the endosperm except at the base of the suspensor.

The development of the endosperm is essentially similar to that of Ranunculus. The endosperm nucleus, fertilized or not, divides successively to form several nuclei distributed throughout the cytoplasm which radiates from them as centers. The antipodal cells number-

ing three, except in one case where four were present, become distinctly separated from the rest of the cytoplasm of the sac. After the first division of the egg cell the endosperm nuclei with their cytoplasm move to the periphery of the sac, where they form a complete lining one cell in thickness. The central portion of the sac is filled with a large vacuole (Pl. II, Fig. 20). The nuclei continue their divisions till the whole sac is filled with endosperm. This occurs about the eight-celled stage of the embryo.

There is considerable variability in the time when the walls appear, but it can be safely stated that they generally appear a little after the eight-celled stage of the embryo (Pl. II, Fig. 22). However, they may occur when the sac is lined with the single layer of nuclei. The antipodals can still be seen, but are on the road to degeneration. In one case I found a peculiar condition of the endosperm. At one end of the sac were the antipodals and at the other the synergids and egg-cell. Scattered in the cytoplasm of the central portion were three large, oval, endosperm nuclei containing several large nucleoli. One of them was dividing amitotically.

The endosperm nuclei, like the pollen mother cells, always divide simultaneously. There is a rhythmical succession of activities. This rhythm is so closely followed that every nucleus is found in the same phase of mitosis at the same time. This condition is localized in individual embryo sacs and there must be, therefore, a mutual reflex stimulus among the nuclei of a given sac.

As the embryo sac proceeds in its development the cells of the nucellus degenerate (Pl. II, Fig. 14). By the time fertilization takes place all have disappeared except the original epidermal covering of the nucellus (Pl. II, Fig. 18). At this stage the seed coats which possess three or four layers of cells have grown considerably beyond the nucellus to form the micropyle. When the endosperm nuclei take a peripheral position, the original epidermal layer begins to degenerate, except a few cells

at the base of the suspensor (Pl. II, Fig. 20). The walls of the cells composing the innermost layer of the seed coats become somewhat thickened and rounded. Later the cells increase greatly in size and become very stony in texture. All the other layers except the external one, which forms a delicate membrane, disappear.

By some botanists Myosurus has been considered a low type from which the monocotyledons and dicotyledons took their origin. This view was based principally upon its external vegetative structure. If it stands on the border line between these two groups, one would expect to find in its embryology features common to both and perhaps one well-developed cotyledon and another rudimentary one. But this is not the case. The cotyledons from their first appearance clear through the period of germination are exactly equal. And, furthermore, the other features of development are typically dicotyledonous, corresponding to those of the other Ranunculaceæ. It is, however, to be regarded from its embryological and vegetative fatures as one of the lowest, if not the very lowest, of the dicotyledons.

This work was carried on in the department of botany of the University of Nebraska, under the direction of Dr. Charles E. Bessey, to whom I am indebted for his interest and assistance.

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EXPLANATION OF PLATES

Drawings were made with camera lucida. For clearness, all figures of pistils or their parts are placed on the page in the same relation to the drawing of the flower (Fig. 8) as exists in nature between the flower and the parts here represented.

PLATE I

FIG. 1. Cross section of an anther showing the region in which two of the sporangia develop. The cells are now undifferentiated. ×590.

FIG. 2. Cross section of anther showing a single microsporangium. Four mother cells surrounded by the tapetal layer. The cells of the wall are arranged radially. × 590.

" 3. Longitudinal section of anther showing the epidermis, two hypodermal layers of the wall, the tapetum composed of binucleate cells, and two mother spores. × 590.

" 4. Four tetrahedrally arranged microspores within the wall of the spore mother cell. × 590.

" 5. Three microspores just after the dissolution of the mother wall. × 590.

" 6. Still later stage of microspore with a thick wall. The nucleus has not yet divided. × 590.

" 7. Mature microspore showing the large round tube nucleus and a generative nucleus. The three thin spots in the wall are visible. × 590.

" 8. Longitudinal section through a young flower. *A*, anther. *B*, petal. *R*, receptacle. *S*, sepal. *P*, pistil. *N*, nucellus. × 35.

" 9. More highly magnified anlage of a pistil. × 365.

" 10. A little later stage showing the anlage of the ovule. × 365.

" 11. The nucellus has bent downwards 90°. The seed coat is appearing at the left, and four megaspores are present. × 365.

" 12. Two-celled stage of the embryo sac. Seed coats appear at the sides. × 365.

" 13. First appearance of archesporium. The pistil has bent upwards to enclose the nucellus. × 210.

PLATE II

FIG. 14. Four-celled stage of the embryo sac. The seed coats have grown to the end of the nucellus. The cells about the sac are degenerating. × 365.

" 15. Mature pistil and embryo sac with its three antipodals, two synergids, egg nucleus and endosperm nucleus. The dotted lines show the position of the fibero-vascular bundles. × 45.

" 16. The stigma of Fig. 15 highly magnified. × 210.

" 17. Embryo sac showing the three antipodals, the two synergids and egg nucleus, and in the center the other two nuclei fusing. × 365.

" 18. The pollen tube entering the embryo sac. The tube nucleus and two generative nuclei are present. The definitive endosperm nucleus is not yet formed. The synergids are degenerating. × 340.

" 19. Pollen tube within embryo sac. Its end, containing two generative nuclei and tube nucleus, is between the large endosperm and the smaller egg nucleus. The degenerating synergids are shown at the side. × 590.

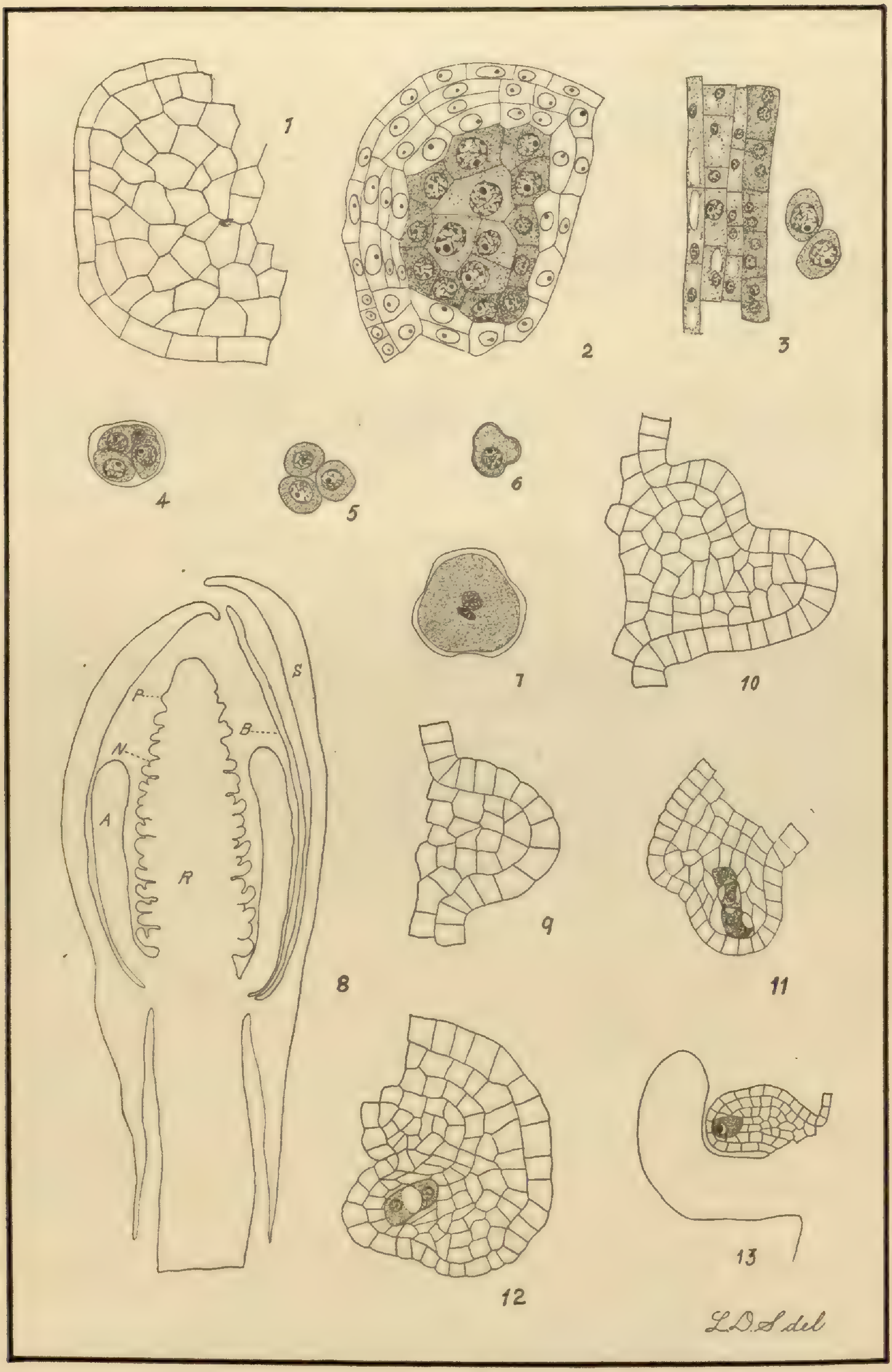
" 20. Eight-celled stage of the embryo. Three cells present in the suspensor. The endosperm nuclei are in the periphery of the sac. Three scattered nuclei of the degenerated nucellus still apparent, only five cells of the epidermal covering being left as a support for the suspensor. × 340.

" 21. A little later stage of the embryo. The distal cell of the suspensor has divided to form four cells, only two of which could be shown. × 340.

" 22. Still larger embryo. In this case there were four cells in the suspensor before the distal one divided to form four. At the left the endosperm with its cell walls is shown. × 340.

" 23. Mature embryo showing two cotyledons and three cells in the suspensor. × 365.

" 24. Surface view of epidermal cells lining the loculus. × 365.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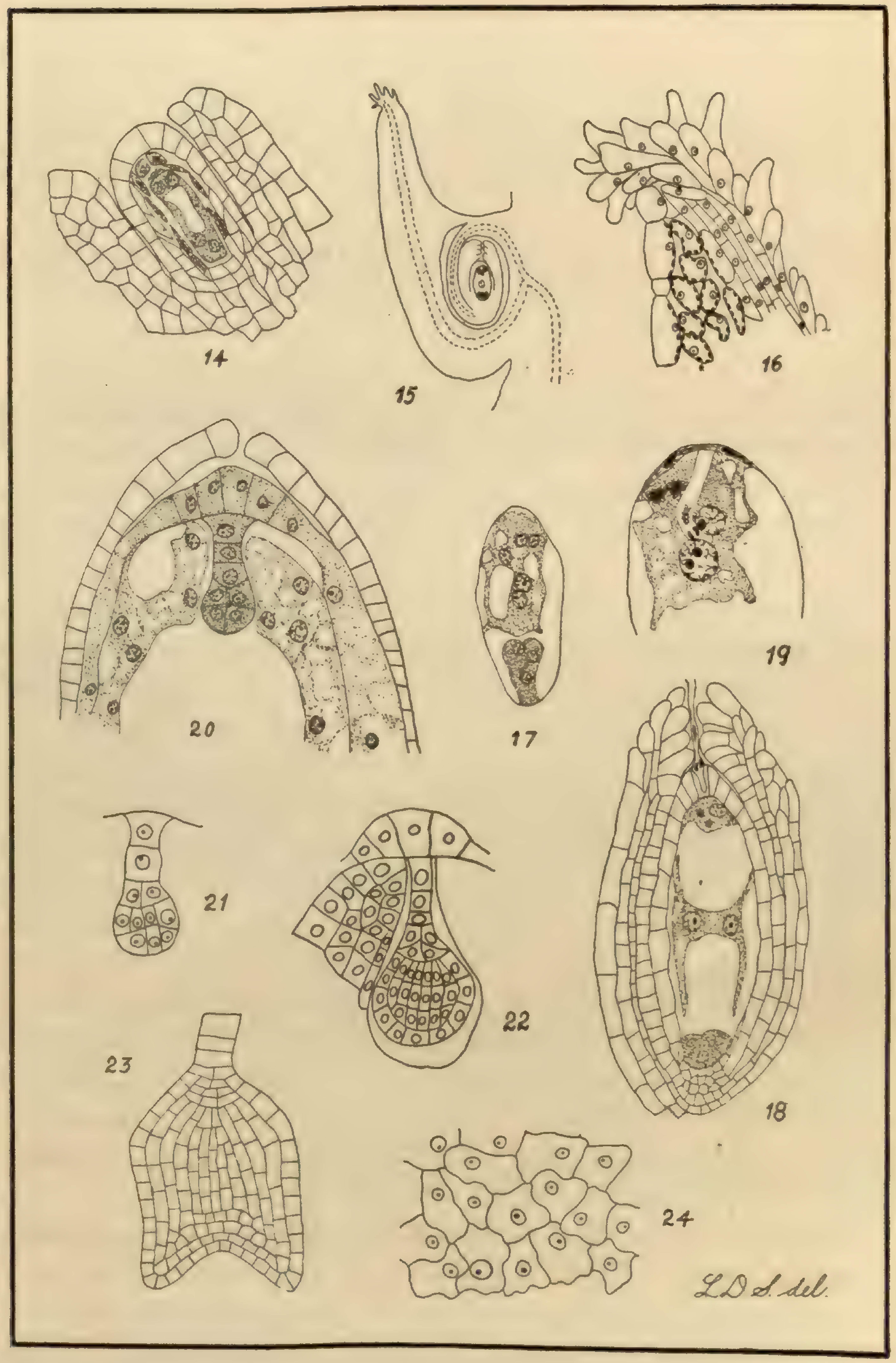
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ANOTHER ASPECT OF THE SPECIES QUESTION

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The American Naturalist for April last (Vol. XLII, No. 496, pp. 217–281) contains a report of the symposium held by the Botanical Society of America at its recent Chicago meeting on "Aspects of the Species Question." This series of eight papers should be of great interest to zoologists as well as to botanists, since it brings so strongly into relief the differences in view-point held by leading taxonomers in two widely different fields of research.

The wide divergence of views here shown in relation to the "species concept" is no less surprising than are the measures urged by some of the speakers for the reduction of "taxonomic anarchy" in botany to some degree of reasonableness. The ecologic botanist needs some method of designating the minor variations which are so important to him in his researches, but from his point of view the question "What is a species?" can be decided only by experimental research. In the meantime we may go on naming forms without essential modification of present methods. From another point of view, the naming of new forms is to be repressed with the utmost rigor, even to the establishment of a "taxonomic censorship" upon "species-making." While most of the speakers appear to agree that there are no species in the Linnean sense, and that species are merely mental concepts, like genera and the higher taxonomic groups, there is a tendency to hark back to the Linnean concept, and to accept the Linnean standard as far preferable to the minute discriminations of modern taxonomers. From other points of view there may be physiological species as well as morphological species; there may be species that

are fixed and immutable, others that yield readily to the forces of environment. That so-called species originate by different methods is evident, thanks largely to modern botanical research. The whole outcome of this symposium, as it affects nomenclature, is naturally indecisive, but contributes a few reasonable suggestions for its improvement. It is, however, a brilliant exposé of conflicting interests and conceptions.

The state of unrest, and the dissatisfaction with the *status quo* here disclosed, are not confined to the ranks of the botanists; the evils here arraigned have long agitated zoologists as well. But the organisms botanists have to deal with are so different from animals, at least the higher forms of animal life, in methods of reproduction, manner of growth, and response to environment, that the species problem in botany is a far more complex question to deal with than it is, for example, in the higher vertebrates, with which alone the writer claims familiarity.

Where to leave off naming "forms" is, after all, the main point at issue, and the next, how best to express their relationships as regards origin and degree of affinity. Utility should be, of course, the criterion in both cases, but especially in the former. How to designate the minor forms, and to what extent they may be profitably provided with names are questions that agitated zoologists apparently long before they became serious problems with botanists. Zoologists, certain of them at least, long since reached what seemed to them a satisfactory solution of the species question by recognition of the fact that "species," like genera and the higher groups, have no real existence, but are merely man-made concepts, purely arbitrary and conventional, devised for convenience in recording our knowledge of organic nature. More than thirty years ago this concept found practical recognition among American ornithologists and mammalogists, and from this hotbed of heterodoxy the infection rapidly spread until this point of view became the working basis

of their coworkers throughout the world. As early as 1884 this postulate was incoroprated in the A. O. U. Code of Nomenclature (first published in 1886), as a reason for the adoption of trinomials, in the following words:

> Recognition of the scientific fact, that a "species," so-called, is not a fixed and special creation, as long supposed, but simply a group of the same intrinsic character as that called a genus, though usually less extensive, and always of a lower taxonomic rank, has done more than any other single thing to advance the science of zoology; for the whole theory of evolution turns, as it were, upon this point.

Respecting the meaning and function of the trinomial system, it is said in the same connection:

> Trinomials are not necessarily to be used for those slightly distinct and scarcely stable forms which zoologists are in the habit of calling "varieties"; still less for sports, hybrids, artificial breeds, and the like; nor indeed to signalize some grade or degree of difference which it may be desired to note by name, but which is not deemed worthy of a specific designation. The system proceeds upon a sound scientific principle, underlying one of the most important zoological problems of the day,—no less a problem than that of the variation of animals under physical conditions of environment, and thus of the origin of species itself. The system is also intimately connected with the whole subject of the geographical distribution of animals; it being found, as a matter of experience, that the trinomial system is particularly pertinent and applicable to those geographical "subspecies," "races" or "varieties" which have become recognizable as such through their modification according to latitude, longitude, elevation, temperature, humidity, and other climatic conditions. It is obvious, therefore, that the kind or quality, not the degree or quantity, of difference of one organism from another determines its fitness to be named trinomially rather than binomially. In a word, *intergradation* is the touchstone of trinomialism.

A small amount of difference, if constant, was considered "specific," in a proper sense, while a large amount of difference, if found to lessen and disappear when specimens from contiguous faunal areas were compared, was considered as not specific.[1]

While these distinctions and principles have been found to work well in vertebrates, and have become to a

[1] Cf. A. O. U. Code of Nomenclature and Check-list of North American Birds, 1st ed., 1886, pp. 27, 31, and context.

large extent the working basis of zoologists, it is evident that they must necessarily fail to meet the needs of botanists, where the minor differentiations are of such a different character, and where so many and such diverse conditions affect differentiation within groups formerly recognized as species. Botanical nomenclature evidently must remain a makeshift, satisfactory to no one, until the ecological, physiological and experimental botanists have come to a better understanding of the causes and relations of morphological and physiological differences among closely related forms.

The introduction of trinomial nomenclature into zoology, while satisfactory for the designation of intergrading geographic forms, left still unsettled the old question of how far it is profitable to recognize in nomenclature the minor morphologic differentiations. In the cases of mammals and birds it was found necessary to reduce many so-called species to subspecies, and also to add, as material increased, many new forms under trinomial designations. These were, of course, intergrading forms, and hence arose the serious question of where to stop bestowing names upon slight morphologic variations, restricted to limited and not very clearly defined physiographic areas. As no hard and fast rule can be formulated, the treatment of such cases becomes largely a matter of temperament, experience and good judgment, in other words, the fitness of the taxonomer for his work. As is well known, the American Ornithologists Union has a permanent committee on the nomenclature and classification of North Amrican birds, whose function it is to consider all proposed changes in nomenclature and all proposed additions to the list of North American birds. This committee, consisting of seven members, is reappointed annually, and is subject to change in personnel. Its reports are published from time to time in the form of supplements to the A. O. Check-List of North American Birds, in which are given not only the accepted changes of nomenclature and the additions to the list, but also

briefly the reasons for not accepting certain of the proposed nomenclatural changes and additions. While, its authority is, of course, not final, except as regards the A. O. U. Check-List, it can throw the weight of its influence against innovations that in its judgment are detrimental to the best interests of the science. It undoubtedly acts as a powerful deterrent upon ill-considered work, and the general acceptance of its decisions by amateurs and laymen tends to the conservation, in this country at least, of a standard and uniform nomenclature for North American ornithology. It is a mild form of censorship—far less radical and drastic than that proposed by some of the botanists at their recent Chicago meeting.

As already said, the conditions in regard to the nomenclature of minor forms which confront botanists are very different from those met with in the study of terrestrial vertebrates. There is no group in mammals, birds or reptiles comparable in respect to the number, character, and association of its minor forms with Cratægus, Rubus, Aster, Sisyrinchium and numerous other botanical genera, where several recognizable morphologic forms occur in intimate geographic association. In the vertebrate classes named, the forms recognized in nomenclature that occupy the same area are always sharply separated; there is never a question of specific or even subspecific identity, except in the case of migratory birds, where several different geographic subspecies may be found associated in migration, or during the non-breeding season, in districts remote from their respective breeding ranges. Questions of identification arise, not between locally associated forms, but in reference to whether individuals from intermediate areas are referable to one or the other of the several subspecies that occur typically only in adjoining physiographic (faunal) areas. An apparent exception is afforded by the red crossbills (*Loxia curvirostra* group), where a wide range of so-called individual variation is met with, affecting the general size,

to some extent the coloration, and especially the relative size and massiveness of the bill. The extremes of variation in the latter are enormous for the size of the bird. As such individuals occur, however, more or less generally throughout the exceptionally wide (almost continental) range of the species, and are thus not characteristic of any particular locality or region, and also are everywhere associated with birds of intermediate characters, these divergent "forms" are not considered by ornithologists as entitled to nomenclatural recognition. Some years since a large-sized, large-billed, very red form was described as a subspecies under the name *Loxia curvirostra bendirei,* based on specimens from eastern Oregon. It was long held in abeyance, however, by the A. O. U. Committee, and finally rejected on the ground that no definite or distinctive geographic range could be assigned to it.

This case is cited as an illustration of the wide differences in conditions that obtain in botany and zoology. If the crossbills grew fixed to the soil like plants, and their ecology was equally open to investigation, some cause might be assigned for the development, respectively, of the large-billed and small-billed forms. At present all we know is that the common red crossbill is an exceedingly erratic species, nesting apparently with equal frequency in mid-winter or in summer, and migrating with extreme irregularity as to season and the regions visited, and characterized by an exceptionally wide range of morphologic variation. The variation in the general size of the individual, and in the size of the bill and in coloration may result from different food habits, and the lack of any sharply defined lines of morphologic separation may be due to frequent or habitual interbreeding of the different morphologic strains. The peculiar life habits and general economy of the species seem to hopelessly remove it from the field of experimental research, at least for the present.

Considering utility as the test, the trinomial system

fairly meets requirements in the case of the higher vertebrates; it seems to apply less satisfactorily in the lower animal phyla and in botany. It is admittedly preferable, however, in botany, in a large number of cases, to the binomial method, even where the variation is not geographic, since it denotes close affinity and supposed ancestry. The suggestion of Clements (*l. c.*, pp. 262–264) that, where new names are required, the third term be chosen with reference to the nature and origin of the variant, seems to offer distinct advantages.

It seems probable that the "species concept" in botany, as in zoology, can be settled only by conventional agreement; and the many interests and the diverse fields of research to be considered and harmonized, seem to relegate this desirable event to the remote future. The present diversity of views respecting the desirability and the manner of designating minor forms does not forecast a speedy agreement on even this important phase of the subject. If ever agreement is reached it obviously must come about through concert of action and mutual concessions. No radical scheme of censorship should be seriously entertained; any attempt to restrain the exercise of individual judgment will be strenuously opposed. Each man's work must stand or fall on its merits, in matters of taxonomy as in other fields of scientific research; the insistence on Latin diagnoses is a step in the direction of medieval intolerance, and apparently had its origin in personal jealousies rather than in a desire to advance the true interests of science. The ability to write in a dead language is no measure of a man's ability as a taxonomer, nor of his scientific sanity, nor of his general levelheadedness as a naturalist. As said by one of the participants of the symposium:

> "What constitute sufficient morphological characters [for a species or for a minor form] must be left to the individual judgment."

The proposition to recognize by name species only and to designate minor forms—the subspecies or "races"—

numerically seems to have met with some degree of approval; which is natural, since, at first sight, it seems to present some advantages. But "*Quercus alba* race 2," or "*Draba verna*, race 104," can mean little unless the authority for the race be added as "race 2 Brown," or "race 104 Smith"; since different authors may be at work almost simultaneously upon the same group, so that race 2 or race 10 of A may not be the race thus designated by B, who at the time was ignorant of what A had done. There would be under this new method the same opportunity as at present for synonymy to play its usual rôle, the same necessity for the strict enforcement of the rule of priority. It is thus hard to see how the conditions would be improved by the adoption of a bare numeral in place of a name, which generally has some useful suggestiveness. If the authority for the race must be added to secure absolute definition, as would certainly be necessary in many instances, very little would be gained in point of brevity, and much lost in the way of aid to the memory. Should such a system be adopted and be made retroactive, chaos would hold place for an indefinite period, and the familiar verbal designations of the past, with their historic suggestiveness, would eventually share the fate of the designations of the herbalists of the past centuries. But there is probably little cause for alarm, since any serious attempt to introduce numerical designations in place of trinomials must, in all probability, demonstrate their impracticability. The proposition is more novel than practical, a protest against burdensome conditions rather than a panacea.

Another point brought out in this series of papers, though of perhaps no great importance, invites comment. It is stated (*l. c.*, p. 246):

"If I understand aright, the ornithologists, at least some of them, are willing to assert that species may differ by characters which can not be described by words [laughter]; that is to say, you will know the species when you see it, but you can not describe it in any language by which another person may recognize it. I think that this is not a

joke, but that it is really stated in earnest; because I read it in *Science*. [Laughter.] But I fancy botanists have not gone quite that far."

The author of this statement, which seems to have excited so much merriment, was simply mistaken. It would have had more basis if he had said subspecies, or "forms," instead of species, but even then would have been misleading and unfair. There are plenty of instances, among both birds and mammals, where local forms of a species are perfectly recognizable by any one as morphologically different when directly compared, through very obvious differences in coloration. But shades of color perfectly apparent to the eye are hard to characterize in language, from the fact that the color terms in current use are vague and uncertain, so that different persons may habitually describe the same tones of color in different terms, and use the same phraseology for quite different tints. It is for this reason that direct comparison of specimens is so often necessary; not that the forms themselves are so difficult to distinguish. The statement that "botanists have not gone quite that far" in describing "forms" is hardly borne out by the confession of another participant in this symposium, who says (*l. c.*, p. 240):

"The general result of these attempts to dissect nature has been embarassing because when a subsequent student takes up the group he is wholly unable to determine from any descriptions that can be written where any given individual would have been grouped by the previous author, unless he has access to the actual specimens which the previous author studied," etc.

THE ORIGIN OF THE LATERAL OF VERTEBRATES EYES

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The steps by which the vertebrate sense organs have arisen have been traced in some measure through the evidence afforded by their embryonic growth. In this respect few systems of organs are more homogeneous. It seems to be a well established principle of embryology that all the sense organs of a developing animal shall arise from its outermost layer of cells, the ectoderm, and the fact that sense organs are the chief means by which an animal tests its environment shows that the embryonic source of these organs is not without significance, for what situation is more important for organs adapted to the reception of environmental changes than the outermost surface of the animal that possesses them. These conditions are well illustrated by most of the sense organs possessed by the vertebrates. Our organs of touch have for the most part remained where they were formed in the outermost layer of the skin. The internal ear, which in the great majority of vertebrates is a complicated sac without connections with the skin, is known to arise in individual development as a pocket from the skin secondarily cut off from that layer. Without doubt it is an excessively delicate organ of touch, for hearing and the other sensory activities of the ear seem to be dependent upon the same form of stimulus as touch, except that the kind of stimulus appropriate to the ear is much more refined than that for simple touch. Like the ear, the vertebrate organs of taste and of smell are also probably derived from the skin and in their cases they still retain the primitive connections with the mother layer, for though they are in cavities, these cavities are lined with tissue directly continuous at the mouth of the cavity

with the skin. Thus, excepting the eyes, all the more obvious vertebrate sense organs show immediate and simple relations with the external layer, the skin.

From this standpoint the lateral eyes of the vertebrate are by no means as simple as the other vertebrate sense organs. As has long been known the vertebrate retina, the essential nervous portion of the eye, does not arise directly from the external layer of the animal, but is an outgrowth from the brain. And though the brain arises by involution from the ectoderm and the retina may therefore be said to come directly from that layer, the fact that the retina does not precede the brain in its development but at best differentiates at the same time with the brain, leaves the question of the exact origin of the retina in uncertainty.

Not only is the vertebrate retina, unlike other vertebrate sense organs, not obviously connected with the external ectoderm, but it is also peculiar in the arrangement of its receptive cells, the rod- and cone-cells. In the great majority of sense organs, the receptive mechanism is made up of cells with very marked polarity in that one end of the cell is differentiated as a receiving structure and is directed toward the impinging stimulus, and the other end either tapers into a fibrous process, the nerve fiber, or is in intimate relation with nerve fibers from other cell bodies. In other words, the sense cells are differentiated in that one end serves for reception, and the other for transmission, and the cell is so placed that the receptive end is nearer the source of the stimulus than the transmitting one. In the vertebrate retina this condition is reversed. The light that enters the eye falls first upon the transmitting ends of the sense cells and only after it has passed through these cells does it reach the receptive end. The vertebrate retina is, therefore, appropriately described as an inverted sense organ. Thus the vertebrate eye departs in two important particulars from the other vertebrate sense organs: first, its sensory elements do not arise in any simple or direct way

from the outer ectoderm and, secondly, these elements are inverted in their relation to the stimulus.

As a consequence of these peculiarities of the vertebrate retina numerous theories have been proposed to account for its present condition. It must be quite clear from what has already been stated, that the chances of a simple course of development for the vertebrate retina are not great, and the first theory to be considered emphasizes this feature. This theory was first proposed by Sharp (1885); subsequently it was independently advanced by Béraneck (1890) whose views were supported by v. Kupffer (1894) and especially by Burckhardt (1901). According to this theory the primitive vertebrate retina is what we now recognize as the lens. As is well known, this organ develops as a pocket of ectoderm in the region superficial to the forming eyeball. In its early stages, as v. Kupffer pointed out, it has a striking resemblance to the beginnings of the nose and the ear and its first steps of development recall those of the eyes of many invertebrates. This primitive retina is supposed by the advocates of this theory to be metamorphosed gradually into a dioptric organ and the deeper ganglionic parts are believed to assume receptive functions and thus establish a new retina from tissue that is an outgrowth from the brain. By this process of replacement the primitive retina is converted into a lens and a secondary retina established. It will be observed that while this theory offers an explanation for the lens and for the origin of the retina from a part of the central nervous system, it does not take into account that very striking characteristic of the vertebrate retina, its inversion. Not only is this theory thus defective, but any candid reviewer must agree, I believe, with Keibel that the resemblance that the vertebrate lens has to a sense organ is only of the most superficial kind and that when one attempts to picture the steps whereby a retina is to be converted into a lens and a ganglionic mass into a retina, the difficulties come to be almost insurmountable. For these reasons this theory

has found relatively few advocates and is regarded by many as wholly untenable.

The second general theory, as to the origin of the vertebrate retina, is one which has much more in its favor and which is presented in as complete a form by Balfour (1881) as by any other. It has recently been independently advanced by Jelgersma (1906). According to this view the vertebrate retina originated on the outer surface of the ancestral vertebrate in much the way that the eyes of many invertebrates have been produced. The primitive retinas thus formed were implanted in that portion of the surface of the animal from which the central nervous system was destined to develop and when this was infolded these retinas were carried in with it, and came thus to be involved in the central organ. If the

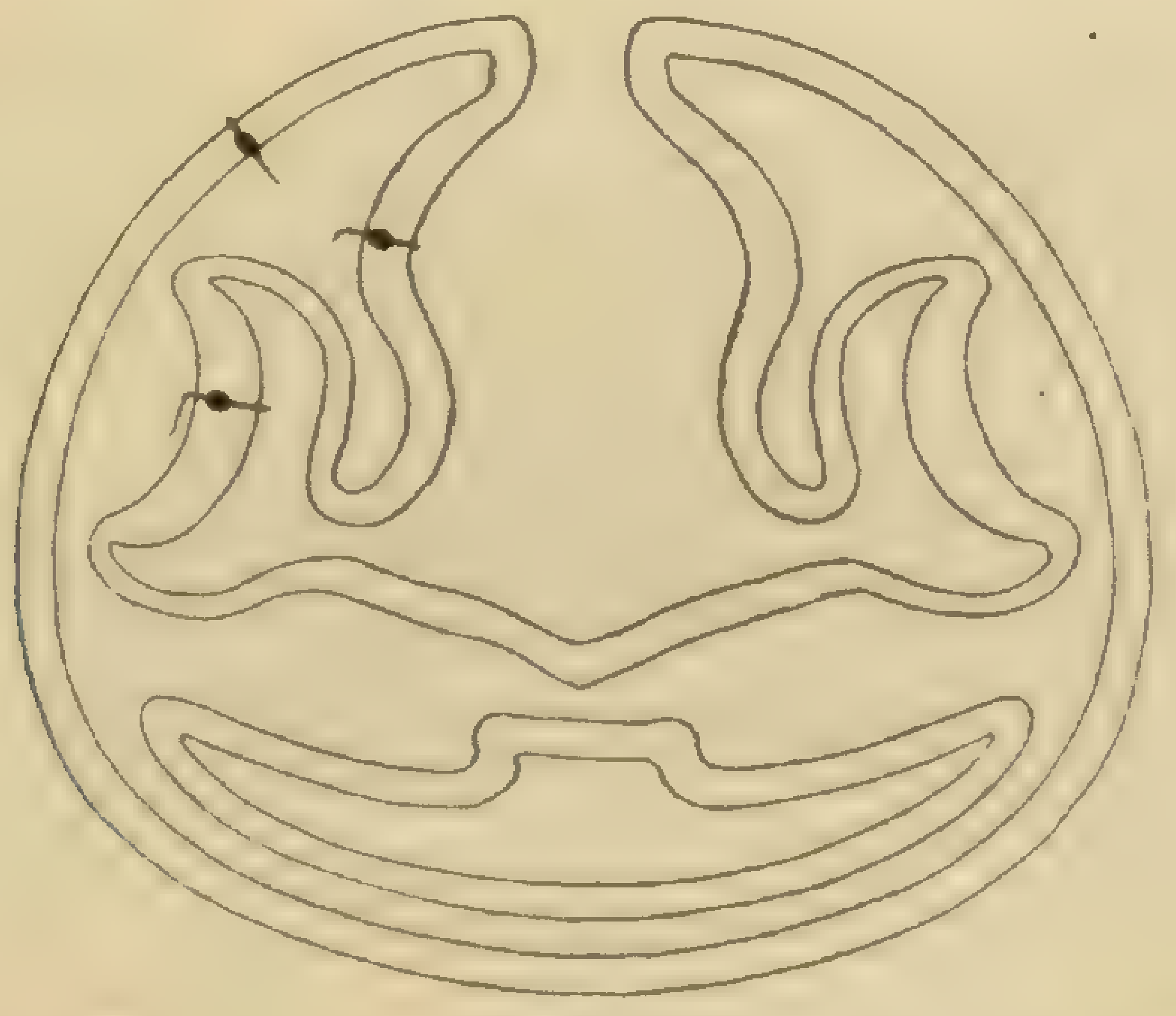

FIG. 1. Imaginary transverse section through the head of a vertebrate embryo to show the morphological relations of the surfaces of the ectoderm of the integument, the medullary tube, and the forming retina. In each of these situations a single sense cell is indicated.

morphological position of a sensory cell such as may have existed in the primitive external retina is supposed to have been retained as this organ was carried from its superficial location into the central nervous system and out again almost to the external surface, the resulting retina would be composed of inverted elements (Fig. 1). Thus this theory at once offers an explanation for the two most striking features of the vertebrate retina, namely, its formation as an apparent outgrowth from the central

nervous system and the inverted condition of its receptive cells.

The most obvious objection to this view is that the retina must be supposed to be a functional organ during this whole process of migration and inversion. But this objection, as others have already pointed out, is not serious, for if we imagine these processes to take place in animals like certain pelagic tunicates or even amphioxus, the transparency of the body would be such as to offer no hindrance whatever to the continuous action of such an organ even when in its deepest position. From this standpoint, therefore, there is no serious objection to the theory as already outlined.

The various adherents of this theory have differed considerably as to the details of its application. The general account of it already given is the particular form which was advocated by Balfour (1881) and which has since been revived by Jelgersma (1906). Balfour makes no mention of any living animal that might be taken to represent, according to this theory, a stage in the evolution of the eye. Von Kennell (1881) designated the annelids as probable ancestors and attempted to show how the external eyes of these worms could be converted into the type of eye found in the vertebrates. Jelgersma on the other hand has accepted amphioxus as an intermediate form and has based his description of the evolution of the eyes on the conditions found in this animal. These three investigators agree in believing that the vertebrate eyes have arisen from optic organs that were once on the exterior of an ancestral form. Lankester (1880) and Boveri (1904), however, do not place the origin of the eye in so remote a region but believed that it arose in the central nervous system in such a place as is now occupied by the eye of the ascidian larva (Lankester) or the numerous eyes of amphioxus (Boveri). In this way these two investigators abandon some very significant parts of the Balfour theory but in other respects they follow it very closely.

Whether we accept the annelids, or amphioxus, or still other animals as representatives of the ancestors of the vertebrates, we shall find it necessary, according to the Balfour theory, to assume some intermediate form in which the eyes are so located as to represent a condition between a primitive integumentary eye and one such as is possessed by the true vertebrates. Such a condition occurs apparently only in the minute larvæ of the ascidians and in amphioxus. As very little is known about the actual conditions in the ascidians in this respect, we shall turn our attention to the optic organs of amphioxus.

Great diversity of opinion has been expressed as to the parts of amphioxus that are sensitive to light. From recent experimental work, however, it may be taken as

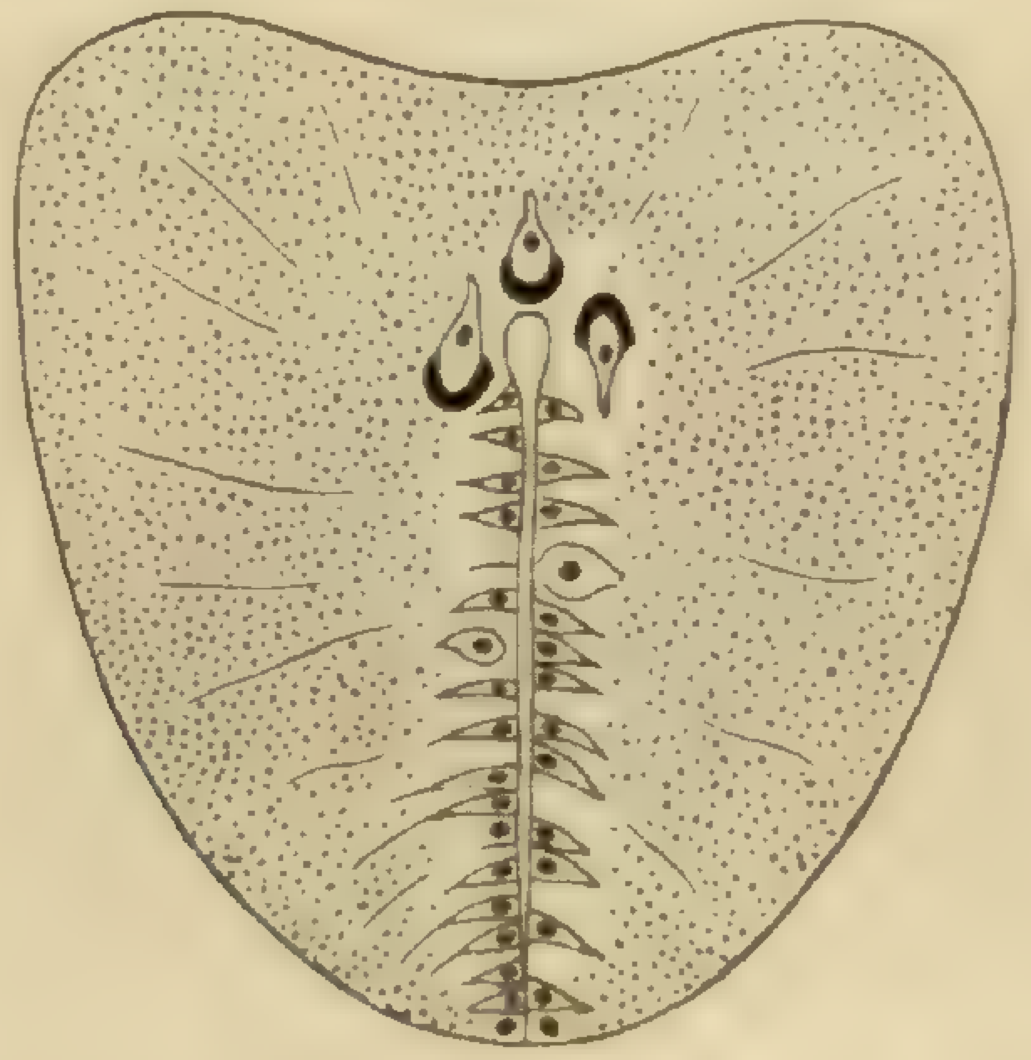

FIG. 2. Transverse section of the nerve tube of amphioxus, showing three direction eyes in place. Modified from Hesse.

fairly well established that the so-called eye-spot at the anterior end of the nerve tube and the integument of amphioxus are not sensitive to light, but that the small pigment cups described by Hesse (1898) as photo-receptive organs and found through almost the whole length of the nerve tube are the true visual organs. They lie in the substance of the nerve tube and though they have not been regarded by Hesse as in any way connected with the vertebrate eyes, they occupy a position that is very suggestive of a stage intermediate between an external eye and one such as the vertebrate now possesses.

Viewed from this standpoint the optic cups of amphioxus are not without interest. They can be seen well in any transverse section of the nerve tube of this animal (Fig. 2) provided the section is not taken from a part of the body too far toward the anterior end. In such a section the cups will be found close to the central canal. Each cup is made up of a concave pigment cell in the hollow of which is a fan-shaped cell. The expanded end of this fan-shaped cell fills the pigment cup while the handle of the fan tapers off into a nerve fiber. The whole structure, as Hesse observed, has a most striking resemblance to the simple direction eye of certain planarians, and it is difficult to resist the conclusion that amphioxus is an animal whose nerve tube is richly provided with a simple type of direction eye.

If these bodies in the nerve tube of amphioxus are direction eyes, their positions are not without significance. On examining a number of transverse sections in which they occur, it will soon be recognized that their arrangement is any thing but regular. Most of them are directed either dorsally or ventrally, but almost any position may be assumed. Though they lie near the central canal, they are not arranged in reference to it with any degree of uniformity. Some point away from it, others toward it.

The lack of uniform arrangement shown by these visual cups is of considerable importance in relation to Balfour's theory of the origin of the retina. If this theory is correct, the inversion of the retina is dependent upon a rigid orientation of the sensory cells which is supposed to have been retained absolutely from their place of origin of these cells in the external skin, through every step in their migration to their final position in the completed retina. If once in the course of this migration orientation is lost, the mechanism fails. Since amphioxus is the only animal that represents well an intermediate stage in this process, and since in amphioxus the orientation *is* lost, it seems to me that Balfour's explanation

falls to the ground. I, therefore, do not believe that the vertebrate retina is inverted because it has been inherited from an integumentary source, and I agree with Boveri that the condition in amphioxus removes all occasion for the assumption that the vertebrate retina arose on the exterior of an ancestral form and became deep-seated by being involved in the developing central nervous system. That the central organs should thus become a seat for the origin of essentially sensory mechanisms is not surprising as long as such an appropriate stimulus as light can in certain cases reach them. Even in our own bodies the respiratory reflex is maintained through the direct stimulation of the medulla by the blood that passes through it, an operation the first step of which must be equivalent to the process of sensory stimulation.

I know of no reason for assuming that the visual apparatus of amphioxus arose in any other than its present position, and I believe there is good grounds, as Boveri has pointed out, for the opinion that the visual cells of amphioxus are the homologues of the rod- and cone-cells of the vertebrates. These visual cells then probably represent the material out of which the vertebrate retina has been made. If this is true why have the eyes of vertebrates developed where they have and how does it come that their retinas are inverted?

An answer to the first of these questions can be found, I believe, in the size of the vertebrate body as compared with that of such an animal as amphioxus. In amphioxus the body is so small and thin that it is sufficiently transparent to allow light to penetrate it anywhere. Hence visual organs may be functional at any point along the length of its nerve tube. In most fishes, however, the increase of size has involved such a development of the body musculature that the posterior part of the nerve tube, the spinal cord, is completely buried in thick, almost opaque tissue. Hence visual cells would no longer be serviceable in such a region as this and they have doubtless thus been restricted to what has become the brain

region of the nerve tube. Furthermore in the brain region the development of the musculature for the gills and jaws together with the growth of the cranium as a support for this musculature must have cut off the light from below. Hence the natural growth of the body of the fish would tend to restrict the occurrence of the visual cells to the sides of the anterior end of the nerve tube, the regions from which the eyes of the vertebrates develop. It is in this partial envelopment of the nerve tube with somewhat opaque tissue that, in my opinion, has limited the eyes of vertebrates to their present positions.

An answer to the second question raised, namely, why is the vertebrate retina inverted, is found, I believe, in the structure of just such direction eyes as amphioxus possesses. The visual cell in each of these eyes has its receptive end buried in the depths of its pigment cup and its fibrous end directed outward through the open mouth of this cup. As the effective light necessarily enters the cup through its mouth, the visual cell is inverted in its relation to this stimulus. If then we imagine a retina to be formed from a great aggregation of individual direction eyes of the type found in amphioxus, it follows that the receptive elements of such a retina would be inverted. This, in my opinion, is the reason for the inversion of the receptive cells in the retina. The vertebrate retina then is fundamentally unlike the other vertebrate sense organs in that it is not directly derived from the external ectoderm, but is developed as a part of the central nervous system, and its inversion is dependent upon its origin from an aggregation of direction eyes each one of which was of necessity inverted from the beginning.

NOTES AND LITERATURE

HEREDITY

Spurious Allelomorphism: Results of Some Recent Investigations.—The original conception of a Mendelian character pair was that of two antagonistic characters, one of which dominates the other in such a way as to prevent the development of the other in individuals inheriting both characters, the *anlagen* of the two being so related to each other in the mechanism of the cell that the pair separates in the reduction division. This conception has recently been modified by leading Mendelian investigators so that now a Mendelian pair is looked upon as presence and absence of a particular Mendelian character, presence being dominant to absence. There are some apparent exceptions to this rule of dominance, but they are probably only apparent.

Some recent investigations indicate that we must still further modify our conception of pairs of hereditary characters. Bateson was the first to call attention to a case[1] which he later[2] terms spurious allelomorphism. It is a case in which two dominant characters behave in transmission as a character pair, *i. e.*, they are alternative in transmission—they can not be transmitted by the same parent to a single offspring. Perhaps, at the outset, we should broaden this conception a little so as to provide for the pairing of any two physiologically unrelated characters, whether dominant or recessive. A suitable term to designate such pairs is needed. The term *appomorphs* would answer the purpose very well were it not for the more or less arbitrary rule of philological *fashion* that hybrid words are not permitted. The first two syllables of this word are Latin, and contain the idea of apposition—the two characters are *apposed* in the reduction division. The last syllable is Greek. Possibly a hybrid word may be permitted in dealing with hybrids unless a good "pure-bred" word can be found.

The first case to which Bateson called attention was that of the erect standard and blue flower color in sweet peas.[3] These two

[1] *Science*, November 15, 1907.

[2] *Science*, May 15, 1908.

[3] *Science*, November 17, 1907.

characters form an alternative pair in the plants with which he dealt. Bateson calls attention to the interesting fact that both are characters of the wild sweet pea. Assuming that in the wild species these characters are transmitted together, we must further assume complete correlation between them; the complex pair thus being blue flowers and erect standard paired with blue flowers and erect standard. The cultivated forms have thus arisen by the loss of erect standard in one member and of the blue factor in the other, leaving the pair consisting of blue flowers on the one side and erect standard on the other. This may be clearer if we express it in formulæ. Let B = the blue flower factor, and E the erect standard. In the wild pea we have BE — BE as the pair of correlated characters, while Be — bE is the form assumed by this pair in the cultivated forms.

The next case of spurious allellomorphism was also found by Bateson,[4] while studying some extraordinary results obtained by Doncaster and Raynor in breeding certain moths (*Abraxas grossulariata* and its var. *lacticolor*). If we let G stand for the character in which the species differs from the variety, and L for the corresponding character in the variety, the results to be explained may be stated as follows:

1. ♀L × ♂G gives only ♀G and ♂G (No L).
2. ♀G × ♂L gives only ♀L and ♂G.

Furthermore, when the male used is a product of either of the above crosses, then

3. ♀G × ♂G gives ♀L, ♀G, ♂G, but no ♂L.
4. ♀L × ♂G gives ♀L, ♀G, ♂L and ♂G.

The following explanation of these phenomena is not given in Bateson's terminology, which seems to the writer to be needlessly involved, but it is based on Bateson's explanation.

Let F = the female character and f its absence.

Let G = *grossulariata* character and g its absence and assume that F and G are allelomorphic to each other.

Result No. 1 above now becomes Fg × GG = FG + GG, or female G and male G.

No. 2 becomes FG × gg = Fg + Gg, or female L and (heterozygote) male G.

No. 3. FG × Gg = FG + Fg + GG + Gg, or female G, female L, and male G.

No. 4. Fg × Gg = FG + Fg + Gg + gg, or female G, female L, male G, and male L.

[4] *Science*, May 15, 1908.

It is noteworthy that the male lacticolors produced in these experiments were the first known, all known specimens of the variety having been females. The reason for this is not far to seek. Male L's occur only when female L's mate with heterozygote males. The latter arise (from G parents) only in those matings which produce female L's (see mating No. 4 above). Heterozygote males are therefore as rare as female L's. If 1/n of the female population is L, then 1/n of the male population is heterozygote. The chance that these two shall mate is therefore $1/n \times 1/n = 1/n^2$. Hence, if only 1 female in 1,000 is L, only one male in 1,000,000 is L, which probably accounts for their having escaped the collector.

In the above case the female sex character seems to be paired with G. This is indeed a highly interesting fact, if true, and the results of Doncaster and Raynor leave little room for doubt that it is true. It now seems probable that sex is a property of a particular chromosome.[5] If this is the case, then the G character should also belong to a particular chromosome.

Bateson[5] also calls attention to what appears to be a similar case of allelomorphism between the sex character and a color element, in the case of black pigmentation of silky fowls, when crossed with Brown Leghorns or other fowls with light shanks.

I desire now to call attention to a similar case that has come under my own observation. It is well known to breeders of Barred Plymouth Rock fowls that an occasional black bird crops out in this breed, and that these blacks are invariably females. Mr. J. F. Spilman, of Wentworth, Mo., tells me that he once crossed some Black Langshan males on his Barred Rock females with the result that in the progeny all the females were black and all the males barred. I have also seen, at the Mississippi Experiment Station, some crosses between Barred Rocks and Indian Games in which part of the progeny was black, the remainder being barred. Unfortunately, in this case, no observations were made as to a possible relation between color and sex. While the data just given are insufficient to establish beyond question the following explanation, the explanation is given in the hope that it may stimulate investigation on this point. Let us suppose that the female sex character (F) is paired with the barring element (B). Let f = absence of F and b = absence of B. Then a cross between a female Barred Rock and a male Black

[5] See remarks by Bateson, *l. c.*

Langshan becomes FB $\times$ bb = Fb + Bb, or black (non-barred) females and barred males, as in J. F. Spilman's experiment. It may be plainer to some if we write the above Fb — Bf $\times$ fb — fb = Fb — fb + fB — fb.

Here F is correlated with b, and f with B; that is, in terms of the chromosome theory, the chromosome which carries F does not carry B, and *vice versa*, though these two chromosomes unite in synapsis to form a bivalent chromosome.

The origin of black females from barred parents is, under our theory, the result of mating a barred female with a heterozygote male; thus: FB $\times$ Bb = FB + *Fb* + BB + Bb.

This mating gives half of the females black, the other half and all the males being barred.

But if we mate a homozygote male barred bird with a non-barred female (carrying black color of course), we get BB $\times$ Fb = FB + Bb, both sexes being barred.

The result of this last mating has not yet been demonstrated. The same is true of the next mating, between a heterozygote barred male and a non-barred female, which should give Bb $\times$ Fb = FB + Bb + *Fb* + *bb;* that is, half of each sex black.

Some similar relation undoubtedly exists between a color element and the sex element both in geese and in ducks, for there are certain breeds of geese in which the males are all white and the females all colored; while in ducks certain breed crosses give the males all of one color and the females all of another.

Two very interesting cases of allelomorphism between two physiologically unrelated characters are found in the recently published work of Noorduijn on "Inheritance in Canary Birds."[6] The data given are not quite full enough to permit their complete elucidation, but they indicate clearly a pairing of the sex element (female) with yellow coat color, and also with a factor of the compound (from the Mendelian standpoint) eye color. There are three principal colors in canaries, namely, yellow, cinnamon (brown), and green. Since mating yellow and cinnamon always gives green birds (usually variegated, but part of the body green) we may infer that the green color arises from the combination of yellow and cinnamon, or of characters correlated with these. Noorduijn states that there are three pigments in the feathers of green canaries, namely, yellow, brown and black.

[6] C. L. W. Noorduijn, in *Arch. f. Rass-. u. Gesell.-Biol.*, April, 1908, p. 162 et seq.

In a letter to the writer he states that in a solution of potash the yellow pigment disappears very quickly, the brown somewhat slowly, while the black disappears only after a much longer interval. My interpretation of Noorduijn's results is that yellow and cinnamon color characters in canaries are probably simple Mendelian characters (unit characters), while black is due to the meeting of two Mendelian factors one of which is correlated with cinnamon and the other with yellow. The case is probably more complex than here indicated, for some of the results indicate the presence of factors in addition to those here assumd. The principal results can now be explained by assuming that C (cinnamon or brown) and Y (yellow) are independent of each other, and that the female sex element (F) is paired with Y. Noorduijn's four cases are:

I. C♂ × G (green or green variegated) females gives G♂ and C♀. This cross sometimes gives G♀'s but never C♂.

II. G♂ × C♀ gives both sexes G.

III. C♂ × Y♀ gives G♂ and C♀. Also sometimes G♀ but never C♂.

IV. Y♂ × C♀ gives both sexes G.

In the above no account is taken of variegation, which Davenport has shown to be itself a Mendelian character.[7] The Mendelian formulæ for Noorduijn's four cases now become (remembering that when C and Y occur in the same bird the color is green or green variegated).

I. CCyy × CCFy = CCFy + CCYy.
C♀ G♂

II. CCYY × CCFy = CCFY + CCYy.
G♀ G♂

III. CCyy × ccFY = CcFy + CcYy.
C♀ G♂

IV. ccYY × CCFy = CcFY + CcYy.
G♀ G♂.

This does not account for occasional green females from crosses I and III, from which fact additional factors not here considered are indicated; but the formulæ indicate quite clearly that the sex element is paired with yellow coat color, or possibly with one factor of this color. This assumption is confirmed by Noorduijn's statement that yellow males tend to impress their color

[7] C. B. Davenport. Inheritance in Canaries. Carnegie Institution, 1908.

more than yellow females. According to our assumption this should be the case, since yellow males transmit yellow to all offspring, while yellow females transmit yellow only to their male offspring.

That one factor of the eye color in canaries is allelomorphic to the female sex element is also clearly indicated by Noorduijn's results. He gives only a meager portion of his experimental results on this point, so that the phenomena can not be explained here. There is enough to indicate that the case involves at least three independent Mendelian factors, one of which is correlated with yellow coat color, and hence allelomorphic to the sex element.

W. J. Spillman.

HUMAN ANATOMY

Sexual and Family Variation in Centers of Ossification.—Dr. J. W. Pryor, professor of anatomy and physiology at the State University, Lexington, Kentucky, for several years has been carrying on an investigation of the ossification of the bones of the human carpus, by means of X-ray photographs. He has made a study of over 550 hands, of which 266 were those of girls and 288 those of boys. In numerous instances he has examined the hands of the same individual at different periods, and has also made a study of the ossification of the bones in children of one family compared with those of other families. In a recent article in the *Bulletin of the State University*, Lexington, Kentucky, April, 1908, he has summed up some of the conclusions arrived at in previous publications, and has brought forth new material in confirmation of his more important generalizations. He finds centers of ossification appear earlier and develop faster in the bones of the female than in those of the male, and that this difference is measurable in infancy by days, in early childhood by months, and later by years. The bones of the first child will, as a rule, ossify sooner than those of subsequent children of the same parents. There is considerable difference in the children of different families in the period when centers of ossification appear, but within a given family there is, as a rule, considerable similarity. Variation in the ossification of bones is an heritable trait. The studies of Professor Pryor enable him to give a more accurate table than has hitherto existed of the period when the centers of ossification appear in the carpal bones. The

following table is copied from his last paper (*Bulletin of the State University,* Lexington, Kentucky, April, 1908) to illustrate the rather remarkable difference in the time of the appearance of the centers of ossification in the male and female hand:

TIME OF APPEARANCE OF CENTERS OF OSSIFICATION IN THE BONES OF THE CARPUS

1. Os Magnum (capitatum)	*Female:* between the third and sixth month. *Male:* between the fourth and tenth month.
2. Unciform (hamatum)	*Female:* between the fifth and tenth month. *Male:* between the sixth and twelfth month.
3. Cuneiform (triquetrum)	*Female:* between the second and third year. *Male:* when about three years of age.
4. Semilunar (lunatum)	*Female:* between the third and fourth year. *Male:* when about four years of age.
5. Scaphoid (navicular)	*Female:* at four years of age, or early in fifth year. *Male:* when about five years of age.
6. Trapezoid (multangulum majus)	*Female:* between the fourth and fifth year (preceding trapezium). *Male:* between fifth and sixth year (preceding trapezium).
7. Trapezium (multangulum minus)	*Female:* between fourth and fifth year (preceded by trapezoid). *Male:* between fifth and sixth year (preceded by trapezoid).
8. Pisiform	*Female:* between the ninth and tenth year. *Male:* between the twelfth and thirteenth year.

C. R. B.

PLANT CYTOLOGY

Cytological Studies on Saprolegnia and Vaucheria.—These interesting and important types have been the subject of several investigations dealing with the processes of oogenesis, fertilization, etc., with conclusions at variance in a number of fundamental points. Two papers have recently appeared which should receive careful attention.

Claussen[1] reports upon oogenesis and fertilization of *Saprolegnia monoica,* contributing important evidence on points under dispute through the investigations of Trow and Davis, and pre-

[1] Claussen, P. Ueber Eientwicklung und Befruchtung bei Saprolegnia monoica. *Ber. d. Deut. Bot. Gesell.,* XXVI, p. 144, 1908.

senting a very different account and interpretation of the process of oogenesis.

There is a stage in oogenesis, before the eggs are developed, when the protoplasm forms a peripheral layer enclosing a large region free from protoplasm in the interior of the oogonium. Other authors have believed this region to be a space containing cell sap, and developed by the gathering and flowing together of vacuoles in the center of the oogonium. Claussen describes the accumulation within the oogonium of a slimy substance which he believes to be derived from the degeneration of the cytoplasm. This cytoplasmic degeneration is conceived as proceeding outward until finally the protoplasm lies as a relatively thin layer in the form of a hollow sphere under the oogonium wall. The well-known nuclear degeneration accompanies, according to Claussen, that of the cytoplasm until relatively few nuclei remain in the peripheral layer. This account of an extensive cytoplasmic degeneration to form a region filled with slime in a living active cell is not paralleled, so far as the reviewer is aware, in any cytological studies upon plants, and is likely to require more detailed study of a microchemical character before it will be accepted.

Claussen is convinced in agreement with Davis that there is only one mitosis in the oogonium and not two mitoses with chromosome reduction as reported by Trow. This is an important point, since Trow's view of chromosome reduction during oogenesis is contrary to the rule among plants that the processes of gametogenesis are unaccompanied by chromosome reduction. The species of the Saprolegniales which are sexual probably reduce the chromosome number (doubled by the fertilization of the egg) with the germination of the oospore; the apogamous species never have the double number, since the eggs develop parthenogenetically.

The account of nuclear structure, the mitosis, and their significance for the processes of oogenesis presents a point of view entirely different from both Davis and Trow. Claussen reports a central body in the resting nucleus and at each pole of the intranuclear spindle. He believes that these establish a nuclear structure with polar organization similar to that of Phyllactinia as described by Harper (see review in the July number of the NATURALIST), but on account of the small size of the nucleus the behavior of this central body was not studied in detail. Each

daughter nucleus following the mitosis is accompanied by such a central body, or centrosome, with delicate protoplasmic radiations; the greater number of these daughter nuclei degenerate. The cytoplasm begins to gather around those which survive, and such regions become the egg origins. Each egg origin has then in its interior a nucleus accompanied by a central body with radiations that extend outward in all directions through the cytoplasm. There is finally a cleavage of the cytoplasm between the egg origins and a rounding up of the protoplasm of each to form the egg.

The central body of Claussen with its radiations is very conspicuous at certain stages of oogenesis. Davis believed the structure to be analogous to the coenocentrum of the Peronosporales and to be developed in the cytoplasm without genetic relation to the nucleus. Trow described asters associated with the surviving nuclei of the oogonium and believed them to be accompanied by deeply staining material constituting a body called by him an ovocentrum. The coenocentrum of Davis corresponds to the ovocentrum and egg aster of Trow and to the central body with radiations of Claussen. The views of Claussen are very interesting and the theory is logical, but his observations on the central body are not sufficiently detailed to establish fully his conclusions. The nuclei of the Saprolegniales and Peronosporales have been studied by a number of competent observers who have failed to find a polar organization. However, these nuclei are small and the problem difficult, and further investigation may establish nuclear polarity in these groups of fungi similar to that in the Ascomycetes as determined by Harper. Should such evidence be forthcoming, the subject of nuclear structure and behavior in the Phycomycetes will take on an entirely new aspect of great significance in the explanation of the processes of gametogenesis and fertilization.

Claussen finds that the eggs of *Saprolegnia monoica* are fertilized, thus adding another form to Trow's list of sexual species, and it seems clear that fertilization occurs for a number of species in this group of fungi which is so largely apogamous. There is a single mitosis in the antheridium, with radiations around the central bodies less evident than in the oogonium. The antheridial tubes on entering the oogonium may apply themselves directly to the egg, but more frequently the ends branch and their tips become applied to several eggs. Finally

the end of such a tip opens and a sperm nucleus enters the egg, passing quickly to the female nucleus, which lies in the center and is without an evident central body. The sperm nucleus increases in size until the two fusing gamete nuclei become indistinguishable. The mitoses of oospore germination were not observed. Claussen found no bi- and tri-nucleate eggs in *Saprolegnia monoica* as were reported by Davis for an apandrous form of *Saprolegnia mixta.*

Studies on several species of Vaucheria by Heidinger[2] are reported in a lengthy paper by Heidinger on the development of their sexual organs. The investigation was conducted in the laboratory of Oltmanns and centers around the disputed point as to how the mature oogonium with its one egg comes to contain a single nucleus, when the young oogonium is multinucleate. Oltmanns described the migration or withdrawal into the main filament of all of the numerous nuclei present in the young oogonium with the exception of one, which remained to become the nucleus of the egg. Davis holds that the young oogonium is multinucleate even after the formation of the cross wall, separating it from the parent filament, and that there is a process of nuclear degeneration during which all break down with the exception of a single surviving nucleus that comes to lie in the center of the egg.

Heidinger's conclusions are in agreement with the views of Oltmanns. All of the numerous nuclei except the future egg nucleus are said to leave the developing oogonium and to pass back into the parent filament before the appearance of the cross wall which separates the oogonium from the parent filament. Heidinger finds no process of nuclear degeneration as described by Davis. The egg nucleus, which remains after the process of nuclear migration, lies at first at the tip of the oogonium and is accompanied by a centrosome-like body, with protoplasmic radiations, similar to the central body described by Claussen for the eggs of Saprolegnia; shortly before fertilization this nucleus passes to the center of the egg.

The paper gives many details of the series of events during the period of fructification and describes interesting culture methods. The cytological account is, however, open to criticism. The fixation was in ½–1 per cent. chrom-acetic acid, a very

[2] Heidinger, W. Die Entwicklung der Sexualorgane bei Vaucheria. *Ber. d. Deut. Bot. Gesell.*, XXVI, p. 313, 1908.

strong fluid for such delicate algæ, and there was evidently much shrinkage of the material, as shown in the outlines of the text figures. These latter are not satisfactory, considering the importance of the details which are discussed, and in the opinion of the reviewer are not convincing. There are some fundamental principles concerned in the discussion between Oltmanns and Davis which will require more thorough investigation before final conclusions are likely to be reached. The most important of these concern the history of the developing oogonium after the multinucleate stage, and the factors that lead to the selection of the nucleus which comes to preside over the egg.

Bradley M. Davis.

HOLOTHURIANS

Holothurioidea.[1]—Under the above title Östergren has made a noteworthy contribution to the literature concerning the Holothurioidea. Based upon years of special study of the group, he concludes that in order to estimate the value of an organ in taxonomy and phylogeny, the function of the organ must be completely understood.

Ostergren first discusses respiration, particularly in connection with the enteron as respiratory organ. By means of their dilator muscles, sometimes the œsophagus, but most often the cloaca, functions as a pump to force the water into other parts of the enteron, or into especially developed extensions of the same. The primitive condition is found in the Synaptidæ.

In most of the Elasipoda respiratory trees are lacking, and yet the cloaca is provided with dilators, and doubtless functions as a pump to force water into the enteron. As Ludwig (1889–92) points out, in various members of the Elpidiidæ and Psychropotidæ, a simple unpaired evagination appears as a "rudimentary gill," or water-lung. From such a beginning comes the single, or double, stemmed respiratory trees. Since it is possible to have within a natural genus certain species without water-lungs, others with them rudimentary, and still others with well-developed respiratory trees, Östergren maintains that the presence, or absence, of these organs is of no particular importance in taxonomy.

[1] Östergren, Hjalmar. Zur Phylogenie und Systematik der Seewalzen. Särtryck ur Zoologiska Studier tillägnade Professor T. Tullberg. Upsala. October 12, 1907.

The pedicels have not the same importance for locomotion in sea-cucumbers as in sea-urchins and star-fishes. The sea-cucumber moves by worm-like contractions of the parts of the body. The pedicels on the part temporarily at rest either suck hold of the solid bottom or bore into the slime, and thus serve to give a firm basis from which the other parts of the body may be extended. Östergren (1897) proves that the anchor-like spicules of the Synaptidæ are locomotor. Even in the pedate holothurians, the spicules help to make a firm anchorage for the resting part of the body while the moving part is bent away from the bottom and thus the rough points made by the spicules do not hinder the forward movement. Some sea-cucumbers, like the remarkable Pelagothuria, swim, and in them the pedicels are small and weak.

On the other hand, the Dendrochirotæ, which remain for a long time in one spot, have well-developed pedicels so that they can suck fast to rocks, or algæ, or on soft bottom, burrow into the slime and by means of their suckers ballast themselves with stones and fragments of shells. The pedicels often gather weeds and shells which form a protective mask. In holothurians without pedicels, the spicules serve for this protective function. In very different groups spicules of the same form, albeit actually fundamentally different, may be developed without indicating any natural relationship of the groups. Such, for instance, are the anchors of the Synaptidæ, and the Molpadiidæ. The branching of the calcareous rods is always in a manner best adapted to form the spicule with economy of material.

While admitting that pedicels and tentacles are homologous as external appendages of the ambulacral system, Östergren claims that they are distinctly different, with no connecting links between, and therefore, like Perrier (1902), declines to follow Ludwig's (1889–92) characterization of the Synaptidæ as having tentacle-feet, and no body-feet. On the other hand, he does not follow Perrier in classifying the Molpadiidæ as apodous, but considers the anal papillæ as reduced pedicels which, like similar appendages in the Aspidochirotæ and Dendrochirotæ, have evolved as tactile organs.

Ludwig (1891) proves for one of the Dendrochirotæ, *Cucumaria planci*, and the present writer has shown (Edwards, 1889, 1905) for one of the Aspidochirotæ, *Holothuria floridana*, that the tentacles develop from the radial canals in the same manner

as the pedicels. Furthermore, in *Holothuria floridana* at first the tentacles are provided with terminal suckers and these organs, like the primitive pedicels, are used for locomotion, while in feeding, as in the adult, they push food into the mouth. Admitting that the distal anal papillæ are modified pedicels, I think it is reasonable to consider the proximal oral tentacles as pedicels, only much more modified in the adult, for their special functions.

Östergren imagines the primitive form, or "Stammholothurie," as having had a soft body-wall containing spicules, and with five simple radial muscle bands, interrupting the transverse sheet of muscle. It moved by contractions of the body, and ate slime. The stone-canal was simple and opened on the outside of the skin. There were many pedicels and either ten or twenty tentacles without ampullæ. The calcareous ring had five radialia and perhaps five interradialia. The enteron was in three loops, the third in the right ventral inter-radius. The blood system did not expand into a *rete mirabile.* The posterior end of the enteron developed as a respiratory cloaca but respiratory trees were not present. There were no auditory vesicles. Östergren's primitive form was most nearly related to the present Elasipoda, and from it he shows how the five chief divisions of the class Holothurioidea may have evolved. Östergren employs as the names of these orders, Elasipoda, Aspidochirota, Dendrochirota, Molpadonia and Apoda (Synaptidæ, Chiridotidæ and Myriotrochidæ), and then concludes with a general description of the chief characters of each order.

CHARLES L. EDWARDS.

THE ENTEROPNEUSTA

Recent Literature on the Enteropneusta. 1. *Systematic.*—Spengel has lately given the classification of the Enteropneusta a thorough overhauling.[1] This accepted imperator in the knowledge of the group recognized at the time 31 species, 9 genera and 3 families. Since then 14 species and one genus have been added. Nearly all the new ones have come from the Pacific and Indian Oceans, these two enormous reservoirs of unknown organisms, the exploration of which has but recently begun in earnest. R. C. Punnett's report, The Enteropneusta in the "Fauna and Geography of the Maldive and Laccadive Archi-

[1] Die Benennung der Enteropneusten-Gattungen. *Zoolog. Jahrb.*, 15 Bd., pp. 209–218, 1901.

pelagoes," Vol. II, Part 2, pp. 631–680, 1903, stands first in point of numbers of new forms, 5 species and 1 genus being added in this, all but one coming from the island groups mentioned in the title. The exception, the type of the new genus Willeyia, comes from Zanzibar. Besides the 5 full-fledged new species recognized by Punnett, the 6 varieties of an old species *Ptychodera flava* are interesting. These are based on a statistical study of the 222 specimens in the collections. This is the first effort made to treat any of the Enteropneusta statistically, and is noteworthy on that account if for no other. The author's attitude toward the subject seems practical and sane. He remarks: "I am not here concerned with the question of the statistical method as a criterion of species and varieties. My point is that in the group of animals collectively designated *Pt. flava* there are to be found different positions of organic stability, and in giving to these 'a local habitation and a name' there is no thought of distinguishing by statistical methods between the terms *race, variety* and *species.*" The only question would be as to the sufficiency in number of specimens examined and the structural features considered to justify all these subdivisions in this particular animal, and the question is to be answered only by further examination of more material.

The next largest numerical contribution is from the Siboga Expedition (Studien über die Enteropneusten der Siboga-expedition, Monographie XXVI, pp. 1–126, 1907, by J. W. Spengel). Three fully accredited species are here described. Worthy of note, perhaps of approval, is Spengel's practise, which is specially illustrated in this report, when dealing with certain forms which he finds to differ somewhat from any already recorded species, but yet not sufficiently to warrant giving them full specific rank on the basis of the small evidence at hand. To these he attaches a "provisional" specific name. Three such names are used in this report. They usually designate specimens from a particular geographic locality.

Spengel appears to be ever dubious about the specific identity of specimens of Enteropneusta occurring in widely separated places. Thus in his "Neue Beiträge zur Kenntniss der Enteropneusten," I and II (*Zoolog. Jahrb.*, 1903 and 1904), he examines in great detail specimens of *Ptychodera flava* Eschsch. from Laysan, and concludes that they differ sufficiently from those described by Willey from New Caledonia, to deserve being

treated provisionally, as distinct. Similarly he examines (Beitrag II) specimens from Funafuti and concludes that these are also recognizably different from those from the type locality. We consequently have as "provisional" designations *Ptychodera fl. caledoniensis, Pt. fl. laysanica,* and *Pt. fl. funafutica.* The author points out that while Funafuti (8° 30′ S.) lies between New Caledonia (20° S.) and Laysan (26° N.), *Pt. fl. funafutica* is not intermediate in structure between the other two forms.

One might, perhaps, question the utility of speaking of such designations as provisional when as a matter of fact no zoological name whatever can be confidently claimed to be final. In the reviewer's opinion there is, nevertheless, real merit in Spengel's practise. It seems to him that proof of the tendency of plant and animal kinds to break up into more kinds as soon as ready means of intercommunication is prevented, is so strong that the systematist is generally bound to suspect that specimens from widely separated localities (at least in many groups) are different until they are shown not to be so. This provisional naming might be looked upon as a recognition of this principle.

Another Pacific species is from Japan (On a new Enteropneust from Misaki, Balanoglossus misakiensis, n. sp.)[2] and another Indian Ocean one from the coast of India (Enteropneusta from Madras).[3]

Hardly less notable than the new species from the least explored parts of the sea is the bringing to light of new ones in the best explored parts. Spengel[4] describes a species of Glossobalanus from the Bay of Naples. The author well remarks that it is "sicher aufallend" that a new species represented by a single specimen should stand accredited to shallow water in the immediate vicinity of the Naples Zoological Station.

2. *Development.*—What must be counted as the most important contribution to Enteropneust development that has appeared since Bateson's series of papers, 1884–1886, has just been published by Dr. B. M. Davis (The Early Life-history of *Dolichoglossus pusillus* Ritter.[5] Davis had shown four years earlier that this California species develops without passing through a tornaria stage. *Dolichoglossus* (*Balanoglossus*) *Kowalevskii* of the Atlantic Coast of the United States, the species studied by

[2] *Annot. Zool. japon.*, Vol. 4, 1902, pp. 77–84.

[3] *Quart. Journ. Micro. Sci.*, Vol. 47, 1903, pp. 123–131.

[4] Neue Beiträge III, *Zoolog. Jahrb.*, 20 Bd., 1904, pp. 315–362.

[5] *Univ. of California Publications in Zoology*, Vol. 4, 1908, pp. 187–228.

Bateson, develops directly also, it is hardly necessary to mention. Since the two species are much alike in most other respects as well, the desirability of examining the development of the Pacific species was obvious. The report before us is confessedly incomplete so far as the entire developmental history is concerned. In some of the phases treated it is, however, measurably full and apparently conclusive. The point of most importance perhaps as developmental problems are now estimated, pertains to the origin of the body cavities. Bateson seemed to find these to arise as five diverticula from the archenteron, viz., one anterior which produces the cavity of the pre-oral lobe, or in the final state the proboscis, a pair immediately behind this producing the cavities of the collar region of the adult, and behind these another pair which produces the cavities of the rest of the animal, *i. e.;* of the thoracic and abdominal portions.

Davis finds a radically different course of things. In the embryo studied by him a single anterior pouch arises as in *D. Kowalevskii,* but instead of the two pairs coming directly from the archenteron, the one anterior pouch sends back lateral pockets between the ectoderm and endoderm, and from these there is constricted off first a pair of cavities which correspond to the future collar, and then in turn from the posterior end of this collar pair, a second pair, presumably representing the future cavities of the thoracic-abdominal region of the adult, is cut off. Since Davis's results rest upon the examination of a large number of embryos (about one hundred and fifty series of sections, he tells us), preserved in a variety of ways and cut in various directions, it seems they must be accepted, and so the conclusion reached that either Bateson's interpretation of his sections was seriously erroneous, or that these two species so closely alike in most respects are unlike in this supposedly fundamental point. Davis strongly inclines to the first view and presents cogent reasons for his inclination based on a critical study of Bateson's text and figures.

The bearing of this finding on the problem of the relationship between Balanoglossus and Amphioxus is clear. The supposed similarity of origin of the body cavities has been taken as a leading proof of genetic kinship between the two animals. Davis does not fail to point out that his observations justify the doubts of the correctness of Bateson's conclusions entertained by both Spengel and Morgan and drawn from their studies of tornaria.

While Davis's work greatly weakens one of the strong supports of blood relationship between these two groups, it does not leave this weakening wholly uncompensated. It seems to find a number of striking resemblances between the egg cleavage of this particular enteropneust and that of Amphioxus. But this part of the study is less full and the significance of resemblance in these earlier developmental stages is more problematic. For the character of the correspondences here the reader must be referred to the paper itself.

3. *Ecology and Physiology.*—Ritter and Davis[6] have studied quite fully the movements of a tornaria of the California coast from near the beginning to the end of its pelagic career. A number of interesting facts pertaining to the character of the swimming movements, the correlation of these with its specific gravity, and this again with its structure are brought out.

Davis (paper on the development of *Dolichoglossus pusillus* already referred to) discusses some points on the distribution and migration of this species as dependent upon the movements of the animal during its larval period, and upon tidal action. Davis finds that the breeding time of *D. pusillus* in San Diego and Mission Bays is January and February, and that the fertilized eggs can be obtained from the burrows of the animals at low tide without great difficulty. Particularly noteworthy is the fact that in spite of the absence of a true tornaria, the young animal still does considerable swimming, and that this follows rather closely the general scheme previously found by Ritter and Davis to characterize the swimming of the tornaria of another species above alluded to.

Ritter[7] has studied the movements of the adult *Dolichoglossus pusillus* and a California species of *Balanoglossus* with the special view of gaining a better understanding of the action of the proboscis and skeletal musculatures and the relation of these to the skeleton. The results make it probable that the nuchal skeleton together with the so-called notochord serves not merely as a support for the isthmus, or neck, but also as an axis upon which the muscles of locomotion act, in part at least.

4. *Anatomy.*—The classification of the Enteropneusta is based

[6] Studies on the Ecology, Morphology, and Speciology of the Young of Some Enteropneusta of Western North America. *Univ. of Calif. Publications, Zoology,* Vol. 1, 1904, pp. 171–210.

[7] The Movements of the Enteropneusta and the Mechanism by which they are accomplished. *Biolog. Bull.,* Vol. III, pp. 255–261.

on a thoroughgoing examination of everything in the make-up of the animals, thanks particularly to the standard set by Spengel's splendid monograph of 1893. From this circumstance it follows that anatomical studies on the adults of either old or new species are not likely to yield greatly important new facts. A few points of considerable general interest, however, come from recent work.

The superficial, presumably secondary, metamerism of portions of the body in several species has attracted the attention of most observers. Willey and Spengel have given it special consideration. In no known species is this more strikingly seen, perhaps, than in the Neapolitan one lately described by Spengel. The prominence and regularity of the bilaterally arranged cross-welts or ridges on the ventral side of the genital region as figured by him, are remarkable indeed. It is not likely that these structures have any great significance either phylogenetic or physiological. They are probably in the main growth characters and are interesting on just this account.

In his extensive studies on the excretory organs of annelids and amphioxus some years ago, E. S. Goodrich predicted that a peculiar type of cells observed in these animals and called by him Solenocytes, would on special search be found in the Enteropneusta. Spengel has given attention to this point, with negative results so far. (Beitrag III.)

References may here be made to Spengel's tilts with Arthur Willey on the latter's speculations as to the vertebrate homologies of various Enteropneust organs. For example, Spengel examines with his accustomed thoroughness the dorsal nerve roots of the collar region in several species and treats with quite pungent sarcasm Willey's contention that in these we have the homologues of the vertebrate epiphysis. A fragment of this particular tilt is worth repeating as literature, though it may be questioned whether Willey ever took himself seriously enough in much of his theorizing on these matters to warrant giving his utterances much time under the aegis of real science. "An epiphyseal structure," Willey is quoted as saying, "like an enteropneustic root, can be transformed into an epiphyseal structure like a pineal eye by losing its primary function . . . passing through a condition of pigmentose degeneration . . . and then being rejuvenated by the acquisition of a new function." Then Spengel himself, "wo in aller Welt giebt es eine

Stütze für eine solche Annahme, dass ein pigmentoser Degeneration anheimgefallenes Organ einer Verjüngung durch Erwerbung einer neuen Funktion fähig wäre . . . ???—und dann schliesst gar der Satz, the agens of rejuvenescence being some form of natural selection! . . . heisst das etwa nicht, den Spöttern über die Selektionstheorie Wasser auf die Mühle tragen?! Es wird Einem ja schwindlig, wenn man an diesen babylonischen Turnbau nur denkt!" W. E. RITTER.

VERTEBRATE PALEONTOLOGY

Pelycosauria of North America.[1]—There are few groups of animals at the present day of greater interest to the paleontologist and evolutionist than the extinct air-breathers of the Permian; and, of the Permian vertebrates, those of America, in their abundance, variety and excellence of preservation are easily the chief. As is well known, Professor Case has, for the past ten years or more, given much intelligent attention to the Permian reptiles of America, and especially to the group which he has described in the present handsome memoir as the "suborder" Pelycosauria. And the writer is inclined to think that he is a little too conservative here, for he believes that the structural characters are so diverse, so widely divergent from those of the modern Sphenodon, that to include them both in one and the same order is to hinder rather than advance an intelligent taxonomy of the reptiles. Mr. Case has given in the volume a complete history of the literature of the group, a taxonomic revision, a thorough discussion of the structural characters of the pelycosaurs, and the facts of their range and distribution. He has not, rather wisely, entered very fully into the many philosophical matters that the animals suggest. He expresses the opinion, however, that the pelycosaurs represent a highly specialized and short-lived branch of the rhynchocephalian stem, and in that he will probably have the concurrence of most paleontologists. But, to the writer, this does not seem altogether certain. The group has an abundance of generalized characters in the vertebræ, pectoral and pelvic girdles, cleithra, etc., the specialization consisting, for the most part, in the extraordinary and most bizarre elongation of the vertebral spines, the teeth, etc. His reasons for the grouping he makes are chiefly to be found in the temporal region of the skull; and the writer

[1] Case, E. C. Revision of the Pelycosauria of North America. *Memoir of the Carnegie Institution of Washington*, pp. 1–176, pls. I–XXXV, 1907.

does not think he is expressing too heretical an opinion when he doubts the great importance of this region in the primary classification of the reptiles. The grouping of the reptiles into two subclasses, the Diapsida and Synapsida, based chiefly upon the temporal structure, is rejected by most students of the reptiles, and the very aberrant structure of this region in the pelycosaurs, especially the presence of a "prosquamosal" bone, rather shakes one's faith. However, we are not quarrelling with the author for not going into these doubtful discussions. He has, what is better, given us excellent material for future philosophizing in his full and lucid descriptions and many illustrations. S. W. WILLISTON.

The Conrad Fissure.[1]—Mr. Brown has given us in this paper an excellent critical and descriptive list, well illustrated, of a very important pleistocene bone deposit, especially interesting as located in the southwest. The material, for the most part collected, and it need not be said skillfully collected by the author, is abundant, including seven species of insectivores, two of bats, nineteen of carnivores, as many of rodents, and nine of ungulates, together with several of amphibians and reptiles. Of these he describes a new twenty species and two genera, the more noteworthy of the new genera being one of a new type of saber-toothed cats. Conspicuous for their absence are remains of the large edentates and of the proboscideans, from which the author is inclined to the belief that the former, at least, were not then in existence in North America. That some of the sloths were in existence in South America at that period is more than probable, if we take into account Gryphotherium, and the same logic would exclude the proboscideans from the fauna, which is not at all probable. He also concludes that the fauna was boreal, as indeed would be indicated by the remains of musk oxen. The paper is a valuable addition to our faunal pleistocene literature.

S. W. WILLISTON.

The Ankylosauridae.[1]—Mr. Brown has given us a rather startling restoration of what he believed to be a new family of

[1] Brown, Barnum. The Conrad Fissure, A Pleistocene Bone Deposit in Northern Arkansas, with Descriptions of Two New Genera, and Twenty New Species of Mammals. *Mem. Amer. Mus. Nat. Hist.*, IX, pp. 157–208, pls. XXIV, XXV, 1908.

[1] Brown, Barnum. The Ankylosauridæ, A New Family of Dinosaurs from the Upper Cretaceous. *Bulletin of the American Museum Nat. Hist.*, X, XXIV, pp. 187–201, 1908.

armored dinosaurs from the Hell Creek Beds of Montana. The material, however, upon which he bases his restoration was scanty—too scanty to serve as a satisfactory basis for a restoration—consisting of the skull, a number of vertebræ, a somewhat problematical scapula, and a number of dermal scutes. The dangers of such attempted restorations as the present one on such imperfect material are apparent here, since Ankylosaurus is either very closely allied to or identical with Stegopelta Williston, a genus overlooked by Mr. Brown. And Stegopelta, which is represented by considerable material in the University of Chicago collections, is as closely allied as well may be with Polacanthus Hulke of England, and must go in the same family. A comparison of Nopsca's restoration of Polacanthus, which is essentially correct, save for the skull, will show the real form of Ankylosaurus, very different from that given by Mr. Brown. Stegopelta, moreover, has spines, and the body is covered in large part by small scutes, though there are also large ones, as figured by Mr. Brown; and the tail rings are correctly placed by Brown. The writer has examined the specimen in the British Museum, and is assured of the relationships. Stegopelta will shortly be more fully described and figured by Dr. Moodie.

S. W. Williston.

PARASITOLOGY

The Evolution of Parasitism.—In a recent paper entitled: "The Influence of Symbiosis upon the Pathogenicity of Microorganisms (The Evolution of Parasitism)," Musgrave[1] has brought together some most important items in an extremely suggestive manner. He defines symbiosis as representing all phases of association between living organisms, beginning with commensalism, on the one hand, and including true parasitism, on the other, in which either component is influenced in nutrition, metabolism, production or in some other manner by the presence of the other. While this use of the term is distinctly new and rather at variance with the older usage of van Beneden the meaning of the author is clear. He endeavors to show that symbiotic combinations between microorganisms are responsible for uninterpreted phenomena in the etiology and pathology of disease. Furthermore, he adduces evidence to show that changes is symbiosis may produce changes in metabolism and also, as a result of this,

[1] *Philippine Jour. Sc.*, B 3: 78.

changes in the pathogenic character of parasites and in the susceptibility of hosts. The work of other authors is cited indicating the influence that surroundings have on cultures of bacteria even under experimental conditions and leading to the conclusion that the relation between nutrition, metabolism and production is far more significant than has heretofore been considered in laboratory technique. If such influences modify artificial cultures, there will surely be a much greater effect from the complex conditions surrounding mixed cultures in unknown symbiosis.

Among animal parasites nutrition, metabolism and production certainly are more complicated than with bacteria, and unless this fact is constantly in mind the whole subject of parasitism is apt to be considered along too narrow lines and our specificities to be regarded as too exacting. The question, just as with bacteria, not only involves a study of the interaction between an animal host and animal parasites, but a study of host under constantly varying conditions being acted upon by parasites influenced by an ever-changing environment. A battle, as it were, takes place between two sets of very complex influences, leading to death or disease of the host on the one hand, to destruction or commensalism on the part of the parasite on the other, or finally quite frequently to what Theobald Smith has called a condition of balanced parasitism.

Most suggestive in this direction is the experimental work which has been done with amœba. Chief among the investigators are Musgrave and Clegg, who found that the cultivation of amœba could not be accomplished satisfactorily except in the presence of other living organisms, and this symbiosis is more or less specific although its specific character may be changed both experimentally and probably also under natural conditions.

The author sums up his paper as follows:

"I am convinced that such an evolution of parasitism from an amœbic and bacterial symbiosis, in water or elsewhere in nature, through a beginning or mixed tissue and bacterial parasitism in amœbic ulcers of the colon, to a true tissue parasitism in the internal organs of the body, or even to a blood invasion itself, is a matter of frequent occurrence. The most promising field for laboratory research in the future will be the study of cause and effect, in the complex relations in which they occur in nature, of the interrelation and interaction of micro-organisms with each other and in their environment of complex symbiosis and the ever-changing and multiple conditions found in hosts."

Trypanosomes.—The life history of various trypanosomes has been investigated with great care at the Runcorn Research Laboratory, Liverpool, by J. E. S. Moore and A. Breinl, with several collaborators. The results appear to be uniform and to differ markedly from those of previous work. These authors are unable to make any distinction between the so-called male, female and parthenogenetic forms of Schaudinn and hold that mere varieties in size or even in some morphological features when taken from different parts of the life cycle should not be spoken of under terms which imply conjugation when no such phenomenon takes place so far as is known. *Trypanosoma gambiense* and *T. lewisi* manifest a cyclical metamorphosis corresponding closely to alternate presence and absence of the parasites from the blood. Periods of maxima and minima alternate irregularly and not with the definite chronicity seen in the development of the malarial organisms. The coming of a minimum is accompanied by the formation of latent bodies consisting of nucleus and vesicle enclosed by a delicate covering of cytoplasm. These latent bodies lodge chiefly in the spleen and bone marrow and from them are developed later a new generation of the typical flagellate forms. Associated with the formation of the latent bodies is an interaction, which occurs at or near the maxima, between the extra-nuclear centrosome, perhaps better named the blepharoplast and the nucleus. It is inferred that the real sexual phase occurs within the transmitting insect, although other investigators look upon the rôle of the latter as purely mechanical.

In *T. equiperdum*, which is the cause of dourine, the entire life history is confined to a single animal and not complicated by transfer through an intermediate host. When inoculated in a rat the process appears identical with that outlined above, save that the round forms which occur at the period characteristic of latent bodies possess two long and delicate flagella. There is in the rat but a single maximum which is followed by the death of the host; in horses the parasites are not sufficiently numerous to permit the observer to follow the changes which take place.

H. B. W.

(No. 500 was issued on September 3)

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THE MANIFESTATIONS OF THE PRINCIPLES OF CHEMICAL MECHANICS IN THE LIVING PLANT.[1]

F. F. BLACKMAN, M.A., D.Sc., F.R.S.

The Uniformity of Nature.

Among the phenomena of nature man finds himself to be one of medium magnitude, for while his dimensions are about a billion times as great as those of the smallest atoms that compose him they are also about one billionth part of his distance from the center of his solar system.

From the vantage point of this medium magnitude the man of science scans eagerly the whole range of natural phenomena accessible to him with a strenuous desire for unity and simplification.

By the unwearying study of special sections of this long front of natural phenomena special guiding principles have been detected at work locally. No sooner has this been accomplished than, in obedience to this desire for continuity throughout, such principles have been freely extended on either side from the point of discovery.

Thus, the theory of probability, which dealt at first with so limited an occupation as drawing white and black balls out of an opaque bag, now is known as the only determinable factor in such remote things as the distribution of the duration of human lives and the effect of concentration of the colliding molecules in a solution upon the rate of their chemical change. Again, the principle of evolution discovered among living things has been

[1] Address of the president of the Botanical Section of the British Association for the Advancement of Science. Dublin, 1908.

extended, till to speak of the evolution of societies, of solar systems, or of chemical elements is now but commonplace.

The biologist, with all his special difficulties, has at least the limitation that he is only concerned with the middle range of the interminable hostile front of natural phenomena, and that for him is ordained the stubborn direct attack, leaving the brilliant attempts at outflanking movements to the astronomers on the one wing and the workers at corpuscular emanations on the other.

The atoms and molecules that the biologist has to deal with do not differ from those passing by the same names in the laboratories of chemistry and physics (at least no one suggests this), and their study may therefore be left to others. At the other end of the scale, with astronomical magnitudes we have not to deal, unless indeed we yield to the popular clamour to take over the canals on Mars as phenomena necessarily of biological causation.

In the study of that particular range of phenomena which is the special allotment of the physiologists, animal and vegetable, we have had ever before us the problem of whether there is not here some discontinuity in nature; whether the play of molecular and atomic forces occurring outside the living organism can ever account for the whole of the complexity and correlation of chemical and physical interactions demonstrable within the living structure.

As yet we are of course far from any answer to this question, and no one in a scientific assembly like this will call upon us for prophecies. Yet the subject to which I shall devote my address has a bearing upon this question. I propose to consider a particular aspect of the relation of chemical changes in a test-tube to those taking place in a living growing plant, and this in the spirit of one who craves for continuity throughout natural phenomena.

The point of view from which the chemist regards the reaction taking place in his test-tube has undergone a

change in the last twenty years, a change bringing it more into uniformity with that of the biologist. No longer content with an equation as a final and full expression of a given reaction, the chemist now studies with minutest detail and with quantitative accuracy the progressive stages of development of the reaction[2] and the effect upon it of varied external conditions, of light, temperature, dilution, and the presence of traces of foreign substances.

Perhaps it is too much to believe that this, as it were physiological, study of each reaction is the effect of some benign irradiation from the biological laboratory. At least, however, it is true that it is the modern study of "slow" chemical reactions which has made all this possible, and the living organism consists almost entirely of slow reactions. The earliest studied chemical reactions, those between substances which interact so quickly that no intermediate investigation can be made, did not of course lend themselves to this work, but nowadays whole classes of reactions are known which are only completed hours or days after the substances are initially mixed. To the slow reactions belong all the hydrolytic and dehydration changes of carbohydrates, fats and proteids that bulk so largely in the metabolism of plants and animals, together with other fermentation changes such as are brought about by oxidases, zymases and enzymes in general. This precise quantitative study of chemical reactions has been developing with remarkable acceleration for some twenty-five years, till it is grown almost into an independent branch of science, physical chemistry. This is sometimes called "general chemistry" because its subject is really the fundamental universal laws of the rate of chemical change, and these laws hold through all the families, genera and species of chemical compounds, just as the same physiological laws apply to all the different types of plants.

[2] Modern research has made it clear that reactions conventionally represented by complex equations of many interacting molecules really take place in a succession of simple stages, in each of which, perhaps, only two molecules interact.

Now if these laws are fundamental with all kinds of chemical change they must be at work in the living metabolic changes. If the chemical changes associated with *protoplasm* have any important factor or condition *quite different* from the state of things which holds when molecules react in aqueous solution in a test-tube, then it might happen that the operation of these principles of physical chemistry would be obscured and not very significant, though it is inconceivable that they should be really inoperative.

My present intention, then, is to examine the general phenomena of metabolism in an attempt to see whether the operations of these quantitative principles are traceable, and if so how far they are instrumental in giving a clearer insight into vital complexity.

THE DOMINANCE OF IRRITABILITY IN PHYSIOLOGY.

I think that certain manifestations of these principles are indeed quite clear, though not generally recognized, and that this neglect is largely due to the dominance of what our German colleagues call "Reizphysiologie"—the notion that *every* change in which protoplasm takes part is a case of the *"reaction" of an "irritable" living substance to a "stimulus."* Now this general conception of protoplasmic irritability, of stimuli and reactions was, of course, a splendid advance, the early development and extension of which we owe largely to our veteran physiologist Professor Pfeffer, of Leipzig. Great as is the service it has rendered to many departments of botany, yet in one direction, I think, it has overflowed its legitimate bounds and swamped the development of the physical-chemical concepts which I shall indicate later on. The great merit of the "stimulus and reaction" conception is that it supplies a very elastic general formula for the sort of causal connection that we find occurring in all departments of biology; a formula which allows the phenomena to be grouped, investigated and formally expounded, whether they be the temporary turgor-movements of "sensitive"

plants, the permanent growth movements of tropistic curvatures, or the complex changes of plant-form and development that result from present and past variations of external conditions.

The strength and the weakness of the conception lie in its extraordinary *lack of particularity.* When an irritable cell responds to a stimulus by a reaction nothing is implied about the mechanism connecting the *cause and the effect,* and nothing even about the relative magnitudes of these, but all this is left for special research on the case under consideration. The one natural chain of cause and effect that is recognized to be outside this comprehensive category is that rather uncommon one in which a definite amount of energy of one kind is turned into an equivalent definite amount of energy of another. Here we have a direct "equation of energy," whereas in a reaction to a stimulus we are said to have typically an "unloosing" effect—a liberation of potential energy by a small incidence of outside energy, as in the classical analogies, drawn from completely comprehended non-living things, of a cartridge exploded by a blow, or the liberation into action of a head of water by the turning of a tap.

So elastic a conception may be easily stretched to fit almost any sequence of phenomena with the apparent closeness that argues a bespoken garment. We must therefore be critically on our guard against cases of such sartorial illusion.

The Principles of Chemical Mechanics.

That my consideration of particular cases may be intelligible it seems necessary that I devote a few minutes to outlining the four quantitative mechanical principles which govern every single chemical reaction, though much that I have to say has been drawn from elementary books on physical chemistry.

These four principles are concerned with (1) the nature of the reaction in question; (2) the amount of reacting substances that happen to be present; (3) the temperature

at which the reaction is taking place; and (4) the influence of catalysts upon the reaction.

For the moment we will confine ourselves to the first two matters, and assume that catalysts are absent and the substances at constant temperature.

1. The first principle that we have to consider is that which declares that no chemical reaction is really instantaneous, though the interaction of substances is often so fast that a direct measurement of its rate can not be made; and, further, that every reaction has its own *specific reaction-velocity* which distinguishes it from other reactions. This is expressed by giving to each particular reaction a numerical *velocity coefficient* which is low or high proportionally as the reaction is slow or quick.

2. This coefficient only expresses the actual experimental velocity when the reacting substances are present in *unit* concentration, because difference of concentration is just the most important factor controlling the actual reaction-velocity.

If a solution of a substance A of unit concentration is undergoing change, then to keep this reaction going at its present rate fresh amounts of A must be added continually just to equal the amount removed by the reaction and so keep the substance up to unit concentration. The amount of A that had to be added thus per unit time would give an exact measure of the amount being decomposed, *i. e.*, of the specific velocity of this reaction.

If the reaction were started with A at double unit concentration, then twice as much A would have to be added *per* unit time to keep the reaction velocity constant at the double rate it would have started at.

And with higher concentrations proportionally more A would have to be added. It is therefore shown that the amount of chemical change going on in unit time is proportional to the concentration. This is a most fundamental principle of chemical mechanics, known as the *law of mass*, and it may be stated thus: *the amount of chemical change taking place at any time is always propor-*

tional to the amount of actively reacting substance (or substances) present.

To carry out experiments by the procedure given above is in practise very difficult and the velocities of reactions are never measured by the chemist in this way. In a living organism this continual bringing up of new supplies of material to maintain a constant rate of change is the ordinary way of life, but in the chemical laboratory procedure is different. There, definite amounts of substances are initially mixed in a vessel and the reaction is allowed to progress by itself without further additions. In this case there is a continual falling off of the concentration of the substance, and so a corresponding diminution of the actual reaction-velocity.

In this procedure the diminution of the initial amount of substance can be actually measured by withdrawing small samples at intervals of time and analyzing them. Let us consider a definite example. Cane-sugar can be hydrolyzed, under various conditions, to give two molecules of hexose, according to the equation

$$C_{12}H_{22}O_{11} + H_2O = 2C_6H_{12}O_6.$$

This reaction goes on, though extremely sowly, when an aqueous solution of cane-sugar is kept very hot in a beaker. Suppose we started with, say 128 grams dissolved in a liter of water and traced the diminution of this amount down towards zero by withdrawing samples at intervals of time and analyzing them. If we plotted the sugar-content of these successive samples against the times when they were taken we should get the curve given in Fig. 1. If we call n minutes the time taken for the sugar to diminish from 128 grams to 64 grams, we should find that in the second n minutes the sugar had fallen to 32 grams, after $3n$ minutes to 16 grams, and so on, the amount halving itself every n minutes. Thus the amounts of cane-sugar hydrolyzed in successive equal intervals are 64, 32, 16, 8, 4, 2, 1 grams, amounts in each case just exactly proportional to the quantity of

cane-sugar then remaining in solution, thus exemplifying the law of mass.

Such a curve as *A* in Fig. 1, which changes by a constant multiple for successive units of time (here halving itself every *n* minutes) is known as a logarithmic curve; the velocity of reaction at any moment is exactly indicated by the steepness of the curve at that moment; the velocity is greatest at first and it declines to almost zero as the curve approaches the horizontal at the end of the reaction.

When instead of the decomposition of a single substance we deal with two dissolved substances, *A* and *B*, reacting together, then as *both* of them go on being thus used up, the amount of change must be ever proportional to the mass or amount of *A* present multiplied by the mass of *B* present.

There is a special important case when the amount of, say, *B* is in very great excess of that amount required to unite with the whole of *A*. Then all through the slow progress of the reaction the amount of *B* never becomes reduced enough to make appreciable difference to its mass, and it may be considered as practically constant all along. In such a case the rate of the reaction is found to be proportional simply to the amount of *A* present, and we get again the curve *A*, Fig. 1. Here the amount of *A* may be considered as a limiting factor to the amount of reaction; *B* being in such great excess never falls low enough to take a practical part in determining the velocity.

The case of the hydrolysis of cane-sugar in aqueous solution is just such a case. The water itself enters into the reaction, but so little is used up in relation to the enormous excess present that the amount remains practically constant and the rate of hydrolysis of the cane-sugar is determined only by the amount of the cane-sugar present at any moment.[3]

3. We have now shown how the actual amount of chemical change going on in a solution is determined by the

[3] 128 grams cane-sugar unite with 6.7 grams water in hydrolysis, and in our experiment nearly 1,000 grams of water are present.

combined effect of (1) the specific reaction velocity and (2) the law of mass. We have next to point out that the specific reaction coefficient is not the same under all circumstances, but is affected by variations of external conditions, always by temperature, and generally by the presence of traces of so-called catalysts.

The relation to temperature we will postpone, and proceed to consider our third principle, the acceleration of reaction velocity by *catalytic agents.*

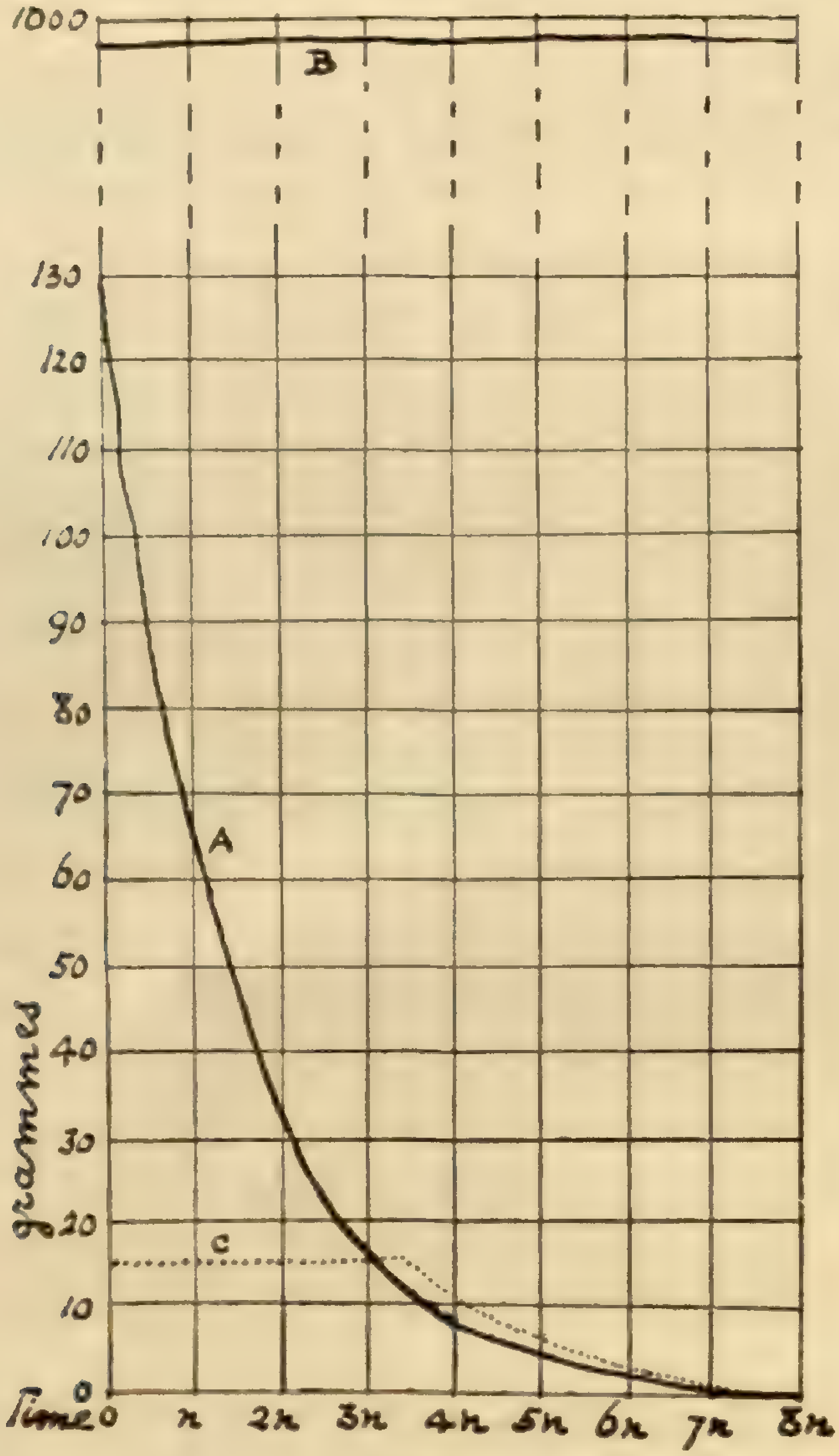

FIG. 1.

It has long been known that small additions of various foreign substances may have a great effect in increasing the rate at which a reaction is proceeding. Thus this hydrolysis of cane-sugar, so slow with pure water, goes at a

fair velocity if a few drops of a mineral acid are added to the solution, while the addition of a trace of a particular enzyme (invertase from plant or animal) enormously increases the rate of change, so that the whole 128 grams of cane-sugar are soon hydrolyzed to hexose. The reaction progresses quantitatively in the same sort of way as before, giving a logarithmic curve of sugar-content. Indeed the same graphic curve, Fig. 1, *A*, would represent the facts if the value of n were reduced from many hundred minutes to quite a few.

The most striking point about this new state of things is that the added body is not used by its action, but the acid or enzyme is still present in undiminished amount when the reaction is completed.

Such actions were at first styled "contact" actions, but are now known as catalytic actions, because we have learned that the catalyst does not work just by contact but by combining with the sugar to form an intermediate addition compound, and that this compound is then split up by the water liberating the catalyst again, but freeing the sugar part, not as cane-sugar, but combined with the water to form two molecules of hexose.

On many chemical reactions, finely divided metals such as platinum and gold have a very powerful catalytic action. Thus platinum will cause gaseous hydrogen and oxygen to unite at ordinary temperatures, and will split up hydrogen dioxide with the formation of oxygen. The intermediate stages in this catalytic decomposition may be summarily simplified to this—

$$H_2O_2 + Pt = PtO + H_2O$$

and

$$PtO + H_2O_2 = Pt + O_2 + H_2O.$$

Thus the reaction goes on and on by the aid of the appearing and disappearing "intermediate compound" PtO till at the end the H_2O_2 is all decomposed and the platinum is still present unaffected.

The enzymes are the most powerful catalytic agents

known, and most of them are specifically constituted to effect the hydrolysis, oxidation, reduction or splitting of some definite organic compound or group of compounds containing similar radicals.

Innumerable enzymes have in late years been isolated from the plant-body, so that it would seem that there is none present to catalytically accelerate each of the slow single changes that in the aggregate make up the complex metabolism of the plant.

The law of mass applies with equal cogency to *catalytic* reactions. If twice the amount of acid is added to a solution of cane-sugar (or twice the amount of enzyme) then the reaction velocity is doubled, and hydrolysis proceeds twice as fast. As the catalyst is not destroyed by its action, but is continually being set free again, the concentration of the catalyst remains the same throughout the reaction; while, on the contrary, the amount of cane sugar continually decreases.

If the catalyst be present in great excess the amount of hydrolysis will be limited by the amount of cane-sugar present, and as this is used up so the reaction will progress by a logarithmic curve as in Fig. 1, *A*. In this case *B* may represent the amount of catalyst. If, on the contrary, there is a large amount of sugar and very little acid or enzyme present, so that the catalyst becomes the limiting factor, then we happen upon a novel state of things; for by the law of mass the rate of hydrolysis will now remain constant for some time till the excess of sugar is so far reduced that it in turn becomes a limiting factor to the rate of change. In this case the velocity curve would consist of a first phase with a straight horizontal line of uniform reaction-velocity leading into the second phase of a typical falling logarithmic curve (see Fig. 1, *C*). These conditions have been experimentally examined by Horace Brown and Glendinning, and fully explained and expounded by E. F. Armstrong in Part II of the critical "Studies in Enzyme Action."[4]

[4] *Proc. Roy. Soc., Vol.* LXXIII, 1904, p. 511.

Having now outlined the three fundamental principles of reaction-velocity, the law of mass, and the catalytic acceleration of reaction-velocity, we are in a position to consider the broad phenomena of metabolism or chemical change in the living organism from the point of view of these principles of chemical mechanics.

THE METABOLISM OF THE PLANT CONSIDERED AS A CATALYTIC REACTION.

Plants of all grades of morphological complexity, from bacteria to dicotyledons, have this in common, that throughout their active life they are continually growing. Putting aside the *qualitative* distribution of growth that determines the morphological form, as a stratum of phenomena above the fundamental one that we are about to discuss, we find that this growth consists in the assimilation of dead food-constituents by the protoplasm with a resulting increase in the living protoplasm accompanied with the continual new formation of dead constituents, gaseous CO_2, liquid water, solid cellulose, and what not. This continual flux of anabolism and katabolism is the essential character of metabolism, but withal the protoplasm increases in amount by the excess of anabolism over katabolism.

Protoplasm has essentially the same chemical composition everywhere, and in the whole range of green plants the same food-materials seem to be required; the six elements of which proteids are built are obviously essential in quantity as building material, but in addition small amounts of Fe, Ca, K, Mg, Na, Cl and Si are in some other way equally essential. What part these secondary elements play is still largely a matter of hypothesis.

Regarding metabolism thus crudely as if it were merely a congeries of slow chemical reactions, let us see how far it conforms to the laws of chemical mechanics we have outlined.

If the supply of any one of these essential elements comes to an end, growth simply ceases and the plant

remains stationary, half-developed. If a Tropæolum in a pot be watered with dilute salt-solution, its stomata soon close permanently, and no CO_2 can diffuse in to supply the carbon for further growth of the plant. In such a condition the plant may remain for weeks looking quite healthy, but its growth may be quite in abeyance.

In agricultural experience, in manuring the soil with nitrogen and the essential secondary elements, the same phenomenon is observed when there is a shortage of any single element. If a continuous though inadequate supply of some one element is available then the crop development is limited to the amount of growth corresponding to this supply. Agriculturalists have formulated the "law of the minimum," which states that the crop developed is limited by the element which is minimal, *i. e.*, most in deficit. Development arrested by "nitrogen-hunger" is perhaps the commonest form of this. All this is of course in accordance with expectation on physical-chemical principles. The quantity of anabolic reaction taking place should be proportional to the amount of actively reacting substances present, and if any one essential substance is quite absent the whole reaction must cease. It therefore seems clouding a simple issue and misleading to say of a plant which, from the arrested development of nitrogen-hunger, starts growth again when newly supplied with nitrogen, that this new growth is a response to a "*nitrogen stimulus.*" It would appear rather to be only the removal of a limiting condition.

Let us now move on a stage. Suppose a growing plant be liberally supplied with all the thirteen elements that it requires, what, then, will limit its rate of growth? Fairy bean-stalks that grow to the heavens in a night elude the modern investigator, though some hope soon to bring back that golden age with overhead electric wires and underground bacterial inoculations. If everything is supplied, the metabolism should now go on at its highest level, and quantities of carbon, nitrogen, hydrogen and oxygen supplied as CO_2, nitrates and water will interact so that these

elements become converted into proteid, cellulose, etc. Now this complex reaction of metabolism only takes place in the presence of protoplasm, and a small amount of protoplasm is capable of carrying out a considerable amount of metabolic change, remaining itself undestroyed. We are thus led to formulate the idea that metabolism is essentially a catalytic process. In support of this we know that many of the inherent parts of the protoplasmic complex are catalytic enzymes, for these can be separated out of the protoplasm, often simply by high mechanical pressure. We know, too, nowadays that the same enzymes that accelerate katabolic processes also accelerate the reverse anabolic processes.

In time a small mass of protoplasm will, while remaining itself unchanged, convert many times its own weight of carbon from, let us say, the formaldehyde (HCHO) of photosynthesis to the carbon dioxide (CO_2) of respiration.

If metabolism is a complex of upgrade and downgrade changes catalyzed by protoplasm we must expect the amount of metabolism to obey the law of mass and to be proportional to the masses of substances entering into the reaction. The case when any one essential element is a limiting factor we have already considered. When all are in excess, then the *amount of the catalyst present* becomes in its turn the limiting factor. Transferring this point of view to the growing plant, we expect to find the limited mass of protoplasm and its constituent catalysts setting a limit to the rate of metabolic change in the extreme case where all the materials entering into the reaction are in excess. When once this supply is available further increase in supplies can not be expected to accelerate the rate of growth and metabolism beyond the limit set by the mass of protoplasm. This, of course, is in accordance with common experience. The clearest experimental evidence is in connection with respiration and the supply of carbohydrates—this, no doubt, because the carbohydrate material oxidized in respiration is normally stored inside plant-cells in quantity and can be estimated. When the

supplies for an internal process have to be obtained from outside, then we have the complications of absorption and translocation to obscure the issue, especially in the case of a higher plant.

Let us first take a case where the carbohydrate supply is in excess and the amount of catalytic protoplasm is small and increasing. Thus it is in seeds germinating in the dark: respiration increases day by day for a time, though carbohydrate reserves are steadily decreasing. Palladine[5] has investigated germinating wheat by analyzing the seedlings and determining the increase of the essential (non-digestible) proteids day by day. The amount of these proteids he regards as a measure of the amount of actual protoplasm present. Assuming this to be so, he finds an approximately constant ratio between the amount of protoplasm at any stage and the respiration.

As germination progresses in the dark the supplies of reserve carbohydrate presently fail, and then the respiration no longer increases in spite of the abundant protoplasm. According to our thesis the catalyst is now in excess and the CO_2 production is limited by the shortage of respirable material.

This second type of case was more completely investigated by Miss Matthæi and myself in working on the respiration of cut leaves of cherry-laurel kept starved in the dark. For a time the CO_2 production of these non-growing structures remains uniform, and then it begins to fall off in a logarithmic curve, so that the course of respiration is just like *C* in Fig. 1. We interpret both phenomena in the same way: in the initial level phase the respirable material in the leaf is in excess, and the amount of catalytic protoplasm limits the respiration to the normal biological level; in the second falling phase some supply of material is being exhausted, and we get a logarithmic curve controlled by the law of mass, as much, it would seem, as when cane-sugar is hydrolyzed in aqueous solution.

After these two illustrations of the action of the law

[5] *Revue gén. de botanique*, Tome VIII, 1896.

of mass from the more simple case of respiration we return to the consideration of the totality of metabolic reactions as exemplified in growth.

What should we expect to be the ideal course of growth, that is, the increase of the mass of the plant regarded as a complex of reactions catalyzed by protoplasm? Let us consider, first, the simplest possible case, that of a bacterium growing normally in a rich culture solution. When its mass has increased by anabolism of the food material of the culture medium to a certain amount it divides into two. As all the individuals are alike, counting them would take the place of weighing their mass. The simplest expectation would be that, under uniform conditions, growth and division would succeed each other with monotonous regularity, and so the number or mass of bacteria present would double itself every n minutes. This may be accepted as the ideal condition.

The following actual experiment may be quoted to show that for a time the ideal rate of growth is maintained, and that at the end of every n minutes there is a doubled amount of protoplasm capable of catalyzing a doubled amount of chemical change and carrying on a doubled growth and development.

From a culture of *Bacillus typhosus* in broth at 37° C. five small samples were withdrawn at intervals of an hour, and the number of bacteria per unit volume determined by the usual procedure. The number of organisms per drop increased in the following series: 6.7, 14.4, 33.1, 70.1, 161.0.[6] This shows a doubling of the mass of bacteria in every fifty-four minutes and is the case actually represented in the strictly logarithmic curve of Fig. 2.

We may quote some observations made by E. Buchner[7] of the rate at which bacteria increase in culture media. *Bacillus coli communis* was grown at 37° C. for two to

[7] Buchner. Zuwachsgrossen u. Wachsthumsgeschwindigkeiten. Leipzig, 1901.

[6] For this unpublished experiment on bacterial growth I am indebted to Miss Lane-Claypon of the Lister Institute of Preventive Medicine.

five hours, and by comparison of the initial and final numbers of bacteria the time required for doubling the mass was calculated. Out of twenty-seven similar experiments a few were erratic, but in twenty cases the time for doubling was between 19.4 and 24.8 minutes, giving a mean of 22 minutes. This produces an increase from 170 to 288,000 in four hours. No possible culture medium will provide for prolonged multiplication of bacteria at these rates.

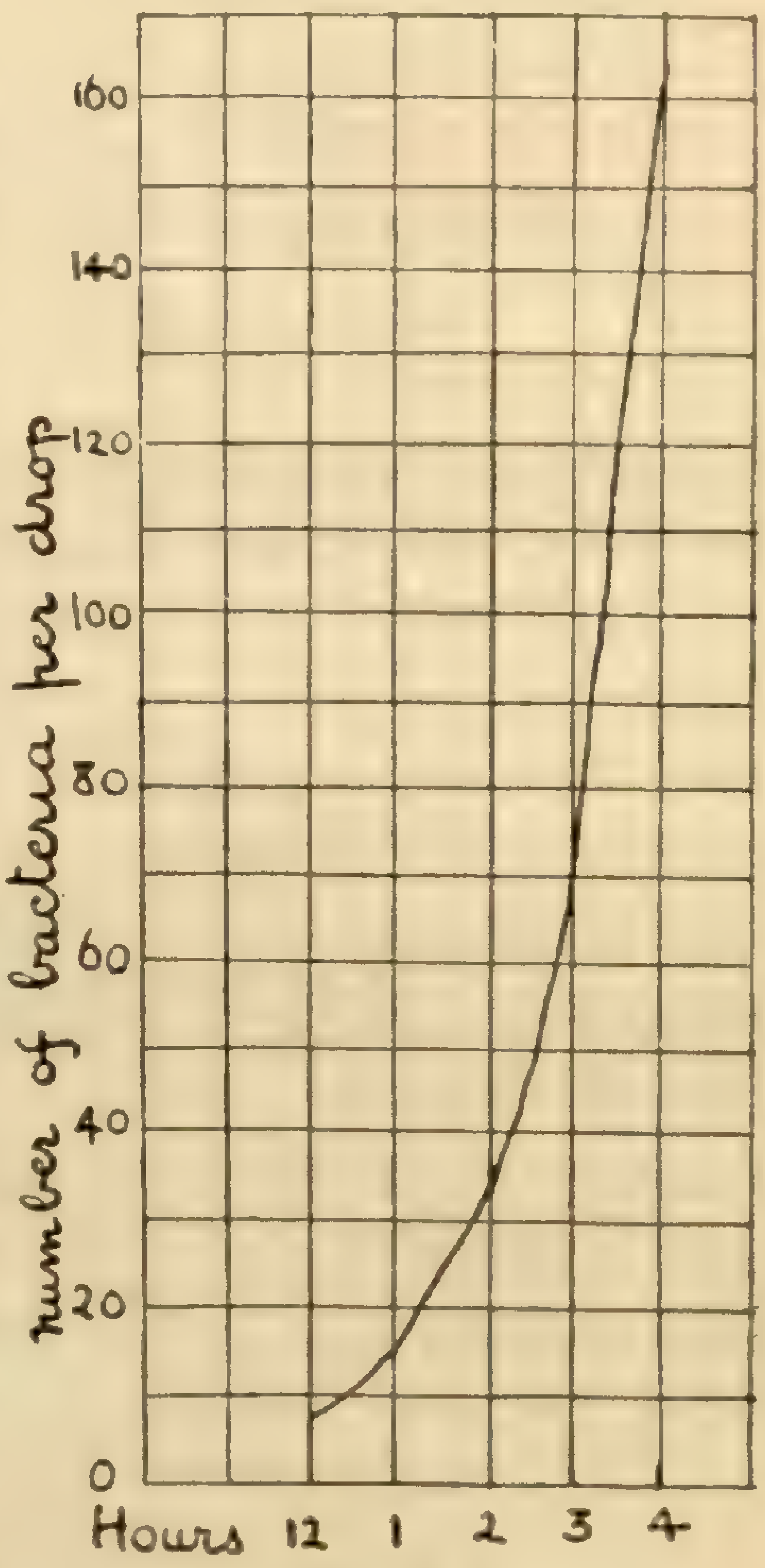

FIG. 2.

Cohn[8] states that if division takes place every sixteen minutes then in twenty-four hours a single bacterium 1 μ long will be represented by a multitude so large that it requires twenty-eight figures to express it, and placed end to end they would stretch so far that a ray of light to travel from one end to the other would take 100,000 years. The potentialities of protoplasmic catalysis are thus made clear, but the actualities are speedily cut short by limiting factors.

For a while, however, this ideal rate of growth is maintained. At the end of every n minutes there is a doubled amount of protoplasm present, and this will be capable of catalyzing twice the amount of chemical change and carrying on a doubled amount of growth and development. This is what common sense and the law of mass alike indicate, and is exactly what this logarithmic curve in Fig. 2 expresses.

This increase of the amount of catalytic protoplasm by its own catalytic activity is an interesting phenomenon. In Section K we call it growth, attribute it to a spe-

[8] Cohn. Die Pflanze. Breslau, 1882, p. 438.

cific power of protoplasm for assimilation (in the strict sense), and leave it alone as a fundamental phenomenon, but are much concerned as to the distribution of the new growth in innumerable specifically distinct forms. In the Chemical Section they call this class of phenomenon "autocatalysis," and a number of cases of it are known. In these a chemical reaction gives rise to some substance which happens to catalyze the particular reaction itself, so that it goes on and on with ever-increasing velocity. Thus, we said that free acid was a catalyst to the hydrolysis of cane-sugar; suppose now that free acid were one of the products of the hydrolysis of sugar, then the catalyst would continually increase in amount in the test-tube, and the reaction would go faster and faster. Under certain conditions this actually happens. Again, when methyl acetate is hydrolyzed we normally get methyl acohol and free acetic acid. This free acid acts as a catalyst to the hydrolysis, and the rate of change continually accelerates. Here, if the supply of methyl acetate were kept up by constant additions, the reaction would go faster and faster with a logarithmic acceleration giving a curve of velocity identical with Fig. 2, *A*.

For a clear manifestation of this autocatalytic increase in the plant it is, of course, essential that the supply of food materials to the protoplasm be adequate.

Another case where we might look for a simple form of this autocatalytic increase in the rate of conversion of food materials to anabolites would be in the growth of a filamentous alga, like Spirogyra. Here, as in the bacterium, all the cells are still capable of growth. In this case the food-material needed in greatest bulk is carbon, which has to be obtained by photosynthesis. Some experiments have been started in the Cambridge Laboratory on the rate of growth of Spirogyra in large tubs of water kept at different temperatures and with varying facilities for photosynthesis and metabolism. Under rather depressing conditions the Spirogyra took several days to double its weight—a rate of metabolism out of all comparison slower than that of bacteria. Experiments on these

lines, with the different food materials as limiting factors, should give instructive results.

We turn now to consider the growth of a flowering plant. Here conditions are more complex, and we know that at the flowering stage or end of the season the growth diminishes considerably. This difference from a simple alga or bacterium we can only regard as a secondary acquisition in relation to the external conditions—either a reaction to a present external stimulus or to the memory of past stimuli. In a flowering plant, too, all the cells do not continue to grow; many cells differentiate and cease to grow and also some of the groups of meristem remain dormant in axillary buds. Clearly the growth curve can not continue to accelerate logarithmically, and in later phases it must tail off; the "grand period" which growth is said to exhibit is another way of stating this. It will, however, be of great interest to us to see what will be the form of the curve of growth during the early period of development.

The importance of this class of work has been realized in Geneva, and detailed work is now being done under the inspiration of Professor Chodat[9] in which the curve not only of growth (fresh weight) but of the uptake of all the separate important elements in selected plants is being carefully followed.

With plants grown in the open, climatic disturbances must occur. We shall therefore figure a curve for the fresh weight of a maize plant grown in water-culture. This is prior to the Geneva work, and due to Mlle. Stefanowska,[10] who has studied also the growth-curves of small animals. The first phase of the curve, lasting some fifty days, shows strictly uniform acceleration, doubling

[9] Monnier, A. Les matières minérales et la loi d'accroissement des végétaux. Geneva, 1905.

Déléano, N. Le rôle et la fonction des sels minéraux dans la vie de la plante. Geneva, 1907.

See also the independent work of Tribot. *Comptes rendus de l'Acad. des Sciences*, October 14, 1907.

[10] Stefanowska. *Comptes rendus de l'Acad. des Sciences*, February 1, 1904.

the weight of the plant every ten days (Fig. 3). The precise external conditions are not stated.

In spite of the morphological complexity the autocatalytic reaction of growth is apparently not checked by inadequate supplies before the plant enters rather suddenly upon the second phase. Here, from the present point of view, we consider that the progress of growth is interrupted, not by the primary physical-chemical causes, but by secondary causes, presumably to be classed in the category of stimulus and reaction.

The numerous curves for the accumulation of different organic and mineral constituents worked out for barley

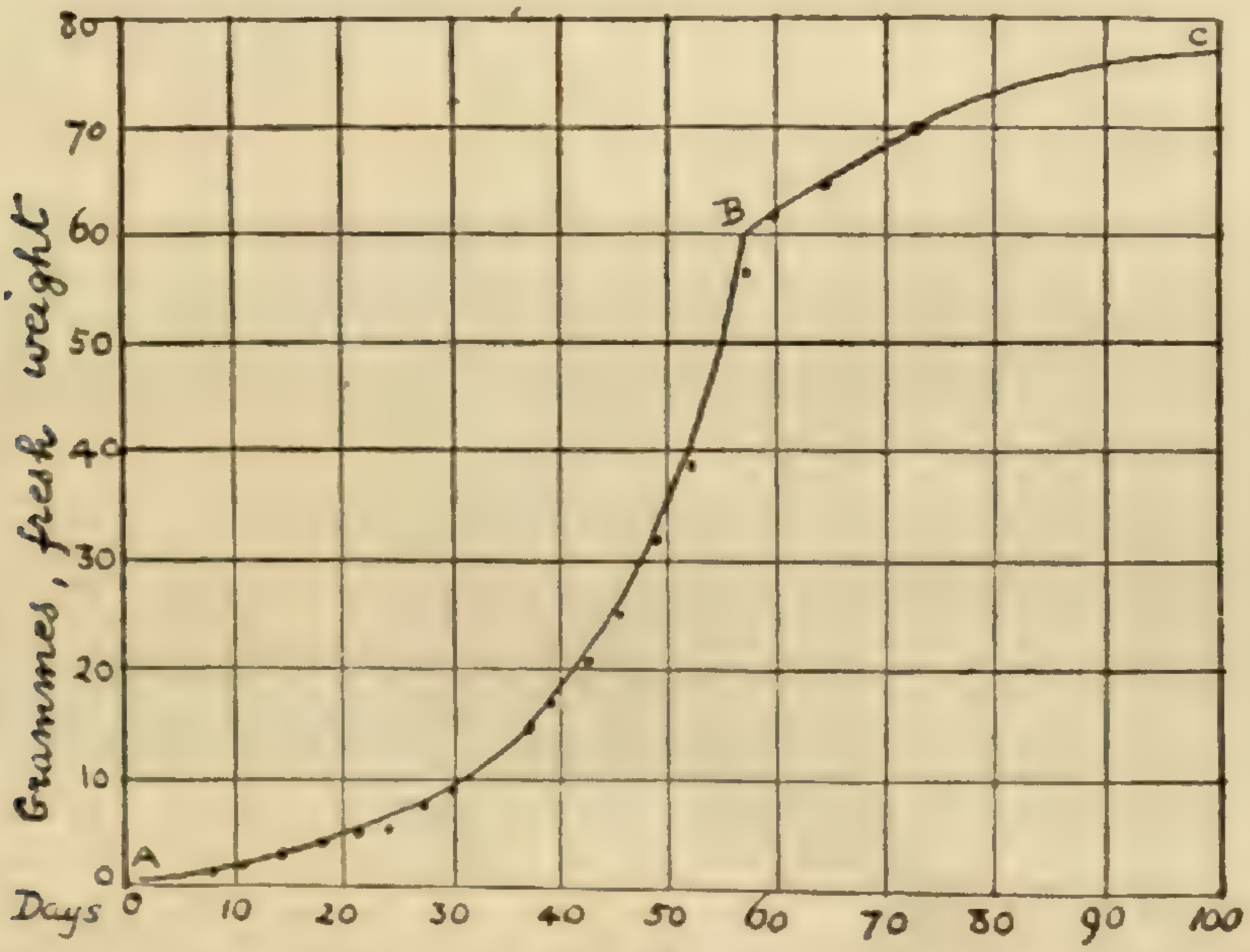

FIG. 3.

and buckwheat at Geneva are of similar form, but do not keep up the uniform rate of doubling so well as does the curve of total fresh weight.

In this connection the tall and dwarf forms of the same plant present an interesting problem, and some experiments have been started on sweet peas at Cambridge. At the time of germination the seedlings weigh about the same, whereas at the end of the season the weight of a tall plant is many times that of a dwarf "cupid" growing alongside under similar conditions. Is the difference due to a less vigorous autocatalysis in the dwarf form, so that throughout its growth it takes a greater number

of days to double its weight? Construction of the curves of growth through the season will show whether it is this or some other alteration in the form of the curve.

I now propose to say a few words about one last point in connection with growth considered as a phenomenon of catalysis before passing on to deal with the effects of temperature.

Of the metallic elements that are essential for the growth of plants some occur in such minute quantities that one can only imagine their function is catalytic. If iron, for instance, played any part in metabolism which involved its being used up in any building material or by-product of metabolism, then a larger amount than actually suffices should be advantageous. If its function is catalytic the iron would go on acting indefinitely without being consumed, and so a minute trace might serve to carry out some essential, and even considerable, sub-section of metabolism.

Elements like manganese, magnesium and iron are often associated with non-vital catalytic action, and a preparation of iron has recently been quantitatively investigated which seems to have literally all the properties of an organic oxydase from plant tissues.[11]

As long ago as 1869 Raulin observed that traces of unessential salts, in particular those of zinc, added to the culture medium in which he grew the fungus Sterigmatocystis caused a rapid acceleration of the growth rate. The time that the mycelium took to double its weight was now reduced to a half or even a third. This continued enormous effect of so small a trace of substance is possibly to be regarded as an added catalyst to the normal protoplasmic apparatus. This sort of effect is currently labeled "chemical stimulation" and has been interpreted as an attempt of the fungus to grow away from an unpleasant environment. To me it looks as if such chemical stimulation were really another example of the in-

[11] Wolff, J. Des péroxydiastases artificielles. *Comptes rendus de l'Acad. des Sciences*, June 9, 1908.

judicious extension of the concept of stimulus and reaction.

This effect of zinc upon the growth of mycelium has recently been verified and extended by Javillier,[12] who has made comparative cultures with increasing doses of zinc salt. He grew Sterigmatocystis for four days at 34° C. in media with graded additions of zinc salts. As the graphic representation shows, he finds a continuous

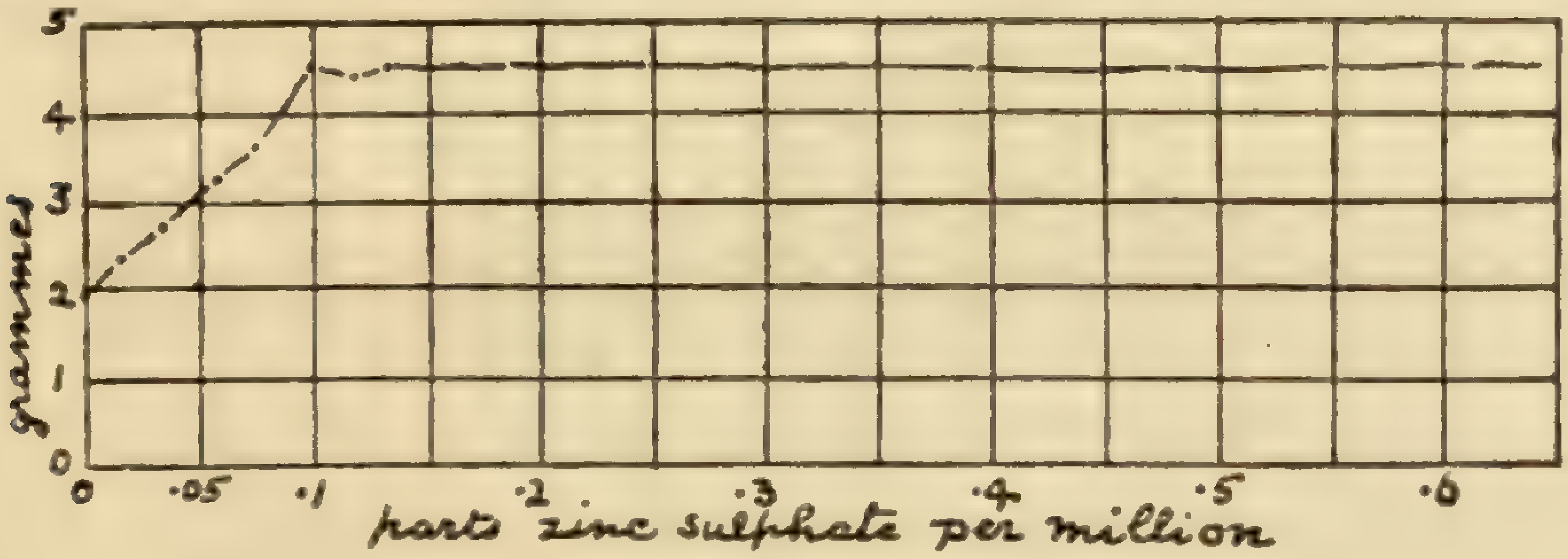

FIG. 4.

regular increase of the number of grams of final dry weight with doses up to 0.00001 per cent., and then no greater but an equal effect up to 100 times as large a dose.

This form of curve with uniform rise at first, abruptly changing to a level top, suggests, as I have pointed out elsewhere,[13] the cutting-off of the primary rising effect by a limiting factor. In this case presumably the limit set by some other sub-section of the metabolism has been attained.

ACCELERATION OF REACTION-VELOCITY BY TEMPERATURE.

We now turn to consider the fourth and last of the principles of chemical mechanics which we might expect to find manifested in metabolism.

It is a universal rule that rise of temperature quickens the rate at which a chemical reaction proceeds. Of course in some rare conditions this may not be obvious, but be obscured by superposed secondary causes; but almost always this effect is very clearly marked.

Further, the nature of the acceleration is a peculiar

[12] *Comptes rendus de l'Acad. des Sciences*, December, 1907.

[13] Optima and Limiting Factors. *Annals of Botany*, Vol. XIX, April, 1905.

one. Rise of temperature affects nearly all physical and chemical properties, but none of these is so greatly affected by temperature as is the velocity of chemical reaction. For a rise of 10° C. the rate of a reaction is generally increased two or three fold, and this has been generalized into a rule by van't Hoff. As this increase is repeated for each successive rise of 10° C. either by the same factor or a somewhat smaller one, the acceleration of reaction-velocity by temperature is logarithmic in nature, and the curve representing it rises ever more and more steeply. Thus keeping within the vital range of temperature a reaction with a temperature factor of $\times 2$ per 10° C. will go sixteen times as fast at 40° C., as at 0° C., while one with a factor of $\times 3$ will go eighty-one times as fast.

This general law of the acceleration of reactions by temperature holds equally for reactions which are being accelerated by the presence of catalysts. As we regard the catalyst as merely providing for the particular reaction it catalyzes, a quick way round to the final stage by passing through the intermediate stage of forming a temporary addition-compound with the catalyst itself, so we should expect rise of temperature to accelerate similarly these substituted chemical reactions.

If this acceleration is a fundamental principle of chemical mechanics it is quite impossible to see how vital chemistry can fail to exhibit it also.

Acceleration of Vital Processes by Temperature.

At present we have but a small number of available data among plants to consider critically from this point of view. But all the serious data with which I am acquainted, which deal with vital processes that are to be considered as part of the protoplasmic catalytic congeries, do exhibit this acceleration of reaction-velocity by temperature as a primary effect.[14]

[14] A collection of twenty cases, mostly from animal physiology, by Kanitz (*Zeits. für Elektrochemie*, 1907, p. 707), exhibits coefficients ranging from 1.7 to 3.3.

Let us briefly consider these data. On the katabolic side of metabolism we have the respiratory production of CO_2, and opposed to it on the anabolic side the intake of carbon in assimilation.

As a measure of the rate of the metabolic processes constituting growth we have data upon the division of flagellates; and finally there is the obscure process of circulation of protoplasm.

The intensity of CO_2 production is often held to be a measure of the general intensity of metabolism, but any relation between growth-rate and respiration has yet to be clearly established. Our science is not yet in the stage when quantitative work in relation to conditions is at all abundant; we are but just emerging from the stage that chemistry was in before the dawn of physical chemistry.

Taken by itself the CO_2-production of an ordinary green plant shows a very close relation with temperature. In the case of the cherry-laurel worked out by Miss Matthæi and myself the respiration of cut leaves rises by a factor of 2.1 for every 10° C. (See Fig. 5, Resp.) This has been investigated over the range of temperatures from 16° C. to 45° C. At this higher temperature the leaves can only survive ten hours in the dark, and their respiration is affected in quite a short time, but in the initial phases the CO_2 output has the value of .0210 gr. per hour and unit weight of leaf, while at 16.2 C. the amount is only .0025 gr. CO_2. Thus the respiration increases over a range of tenfold with perfect regularity solely by increase of temperature. No reaction in a test-tube could show less autonomy. At temperatures above 45° C. the temperature still sooner proves fatal unless the leaf is illuminated so as to carry out a certain amount of photosynthesis and compensate for the loss of carbon in respiration. Thus, with rising temperature, there is at no time any sign of an optimum or of a decrease of the intensity of the *initial* stage of respiration.

Here, then, on the katabolic side of metabolism we have no grounds for assuming that "temperature-stimuli" are at work regulating the intensity of protoplasmic respira-

tion, but we find what I can only regard as a purely physical-chemical effect. The numbers obtained by Clausen[15] for the respiration of seedlings and buds at different temperatures indicate a temperature coefficient of about 2.5 for a rise of 10° C.

To this final process of katabolism there could be no greater contrast than the first step of anabolism, the assimilation of carbon by the protoplasm as a result of photosynthesis. We must therefore next inquire what is the relation of this process to temperature.

This question is not so simple, as leaves can not satisfactorily maintain the high rate of assimilation that high temperatures allow. The facts of the case were clearly worked out by Miss Matthæi,[16] the rate of assimilation by cherry-laurel leaves being measured from −6° C. to + 42° C. Up to 37° C. the curve rose at first gently and then more and more steeply, but on calculating out the values it is found that the acceleration for successive rises of 10° C. becomes less and less. Between 9° C. and 19° C. the increase is 2.1 times, the highest coefficient measured, and exactly the same coefficient as for respiration in this plant, which in itself is a striking point, seeing how different the processes are. (See Fig. 5, Assimilation.)

The decrease of the coefficient with successive rises is a state of things which is quite general among non-vital reactions. A critical consideration of the matter leads one to the conclusion, however, that this failure to keep up the temperature acceleration is really due to secondary causes, as is also the appearance of an optimum at about 38° C. Some of these causes, have been discussed by me elsewhere,[17] and I hope to bring a new aspect of the matter before the section in a separate communication. The conclusion formerly come to was that probably in its initial stages assimilation at these very high tempera-

[15] *Landwirtschaftliche Jahrbücher*, Bd. XIX, 1890.

[16] *Phil. Trans. Roy. Soc.*, Ser. B, Vol. CXCVII, 1904.

[17] Optima and Limiting Factors. *Annals of Botany*, Vol. XIX, April, 1905.

tures started at the full value indicated by a theoretically constant coefficient, but that the protoplasm was unable to keep up the velocity, and the rate declined. It must be borne in mind here that quite probably no chloroplast

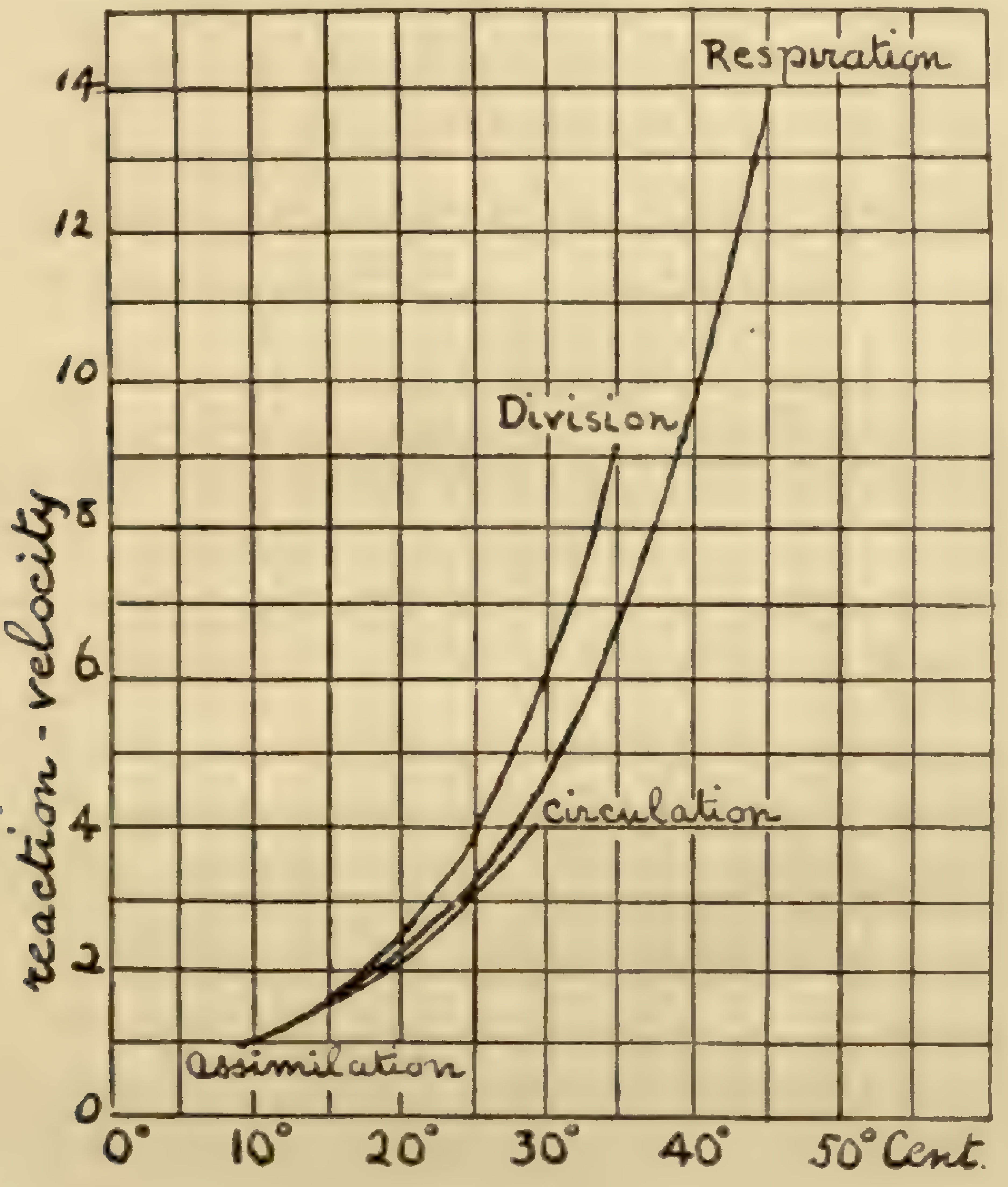

FIG. 5.

since the first appearance of green cells upon the earth had ever been called upon for anything like such a gastronomic effort as these cherry-laurel leaves in question. It is not to be wondered that their capacities speedily declined at such a banquet, and that the velocity-reaction of anabolic synthesis traces a falling curve in spite of the keeping up of all the factors concerned, to wit, temperature, illumination, and supply of CO_2. This decline is not permanent, but after a period of darkening the power of assimilation returns. Physical-chemical parallels can easily be found among cases where the accumulation of the products of a reaction delays the apparent velocity of the reaction, but this complicated case may be left for further research.

In relation to assimilation, then, we must say that

owing to secondary causes the case is not so clear over the whole range of temperature as that of respiration, but that at medium temperatures we have exactly the same relation between reaction-velocity and temperature.

We may consider now some data upon the combined net result of anabolic and katabolic processes. Such total effects are seen in their clearest form among unicellular saprophytic organisms for which we have a few data. Mlle. Maltaux and Professor Massart[18] have published a very interesting study of the rate of division of the colorless flagellate *Chilomonas paramaecium* and of the agents which they say stimulate its cell-division, in particular alcohol and heat.

They observed under the microscope the time that the actual process of division into two took at different temperatures. From 29 minutes at 15° C. the time diminished to 12 minutes at 25° C., and further to 5 minutes at 35° C. The velocities of the procedure at the three temperatures 10° C. apart will therefore be in the ratio of 1 : 2.4 : 5.76, which gives a factor of 2.4 for each rise of 10° C. (See Fig. 5, Division.)

Now we are told by the investigators that at 35° C. Chilomonas is on the point of succumbing to the heat, so that the division rate increases right up to the death point, with no sign of an optimum effect. Below 14° C. no observations are recorded.

Here, then, we have throughout the whole range exactly the same primary temperature relation exhibited by the protoplasmic procedure that we should expect for a chemical reaction in a test-tube.

This division phase is only a part of the life-cycle of the flagellate, and between division it swims about anabolizing the food material of the medium and growing to its full size ready for the next division. One wishes at once to know what is the effect of the temperature upon the length of the life-cycle. Is the whole rate of metabolism quickened in the same way as the particular section con-

[18] Maltaux and Massart. *Recueil de l'Institut botanique Bruxelles*, Tome VI, 1906.

cerned with actual division? Of course a motile flagellate can not be followed and its life-cycle directly timed but the information was obtained by estimating carefully what percentage of individuals was in a state of actual division at each temperature. It was found that always 4 per cent. were dividing, whatever the temperature. This proves that the whole life-cycle is shortened in exactly the same proportion as the process of division at each temperature, and that it is just twenty-five times as long. Therefore the life-cycle is 125 mins. at 35° C. and 725 mins. at 15° C., so that here, again, we have the physical-chemical relation with a factor of 2.4 for each rise of 10° C.

In this paper of Maltaux and Massart these relations are not considered as the manifestations of physical-chemical principles, but are regarded as reactions to stimuli; and the paper contains a number of experiments upon the effect of sudden changes of temperature upon the occurrence of division. As far as one can make out from inspection of the scattered literature, it does seem established that sudden changes of temperature act as stimuli in the strict sense of the word. In many investigations one finds it stated that a quick change of temperature produced a certain reaction which a slow change of temperature failed to evoke. Usually all the phenomena are treated in terms of stimulation, and the absence of reaction with slow change of temperature is regarded as secondary. Were it not for the specific stimulatory effects of quick change, which are not difficult to comprehend as a phenomenon *sui generis,* I hardly think so general a tacit acquiescence would have been extended by botanists to the view that all enduring changes of velocity of metabolism brought about by lasting changes of temperature are stimulatory in nature.

No determination of the rate of development of bacteria through a very wide range of temperature seems to have been made. There are various incidental experiments which indicate values about 2 for the coefficient of increase of metabolism for a rise of 10° C.

I am not acquainted with any data for the growth rate of whole flowering plants at different temperatures: Of course the case of growth most usually measured in the laboratory, namely, where one part of a plant extends at the expense of the reserves stored in another part and there is a decrease, not an increase, of total dry weight, is not the type of growth we have to deal with. Even for simple elongation of a shoot at different temperatures we have but few data. Those of Koppen (1870) generally quoted are wildly irregular, and in many cases it is clear that the growth-extension of complex structures is a process which proceeds by spasms rather than smoothly.

The rate of movement of circulating protoplasm increases rapidly with temperature, but Velten's numbers do not give an obvious logarithmic curve. If we confine our attention to the values for 29° C. and 9° C. we do find, however, that the velocity increases about two-fold for each rise of 10° C. being 10 mm. at 9° C. and 40 mm. at 29° C.

Taken altogether these various data clearly support the hypothesis that temperature accelerates vital processes in the same way as it does non-vital chemical reactions, that is, logarithmically by an approximately constant factor for each rise of 10° C.; and, further, it accelerates them to the same extent; that is, that the factor in question has values clustering about 2–3.[19]

To make these similarities more significant I ought to point out that no other properties of matter are accelerated to anything like this extent by rise of temperature. Most reactions increase in velocity by no less than 10 per cent. per degree rise of temperature; a most marked effect, and yet there is no generally accepted explanation of this almost universal phenomenon. By the kinetic theory of gases each rise of a degree in temperature increases the movements of the gas-molecules, so that the

[19] It has been proposed to use the size of the temperature coefficient to settle whether a process like the conduction of an impulse along a nerve is a chemical or a physical process. See Lucas, Keith. *Journal of Physiology*, Vol. XXXVII, June, 1908, p. 112.

number of collisions between them is greater, but only about $\frac{1}{6}$ per cent. greater. With rise in temperature, too, the viscosity of a solution diminishes, so that there is less resistance to internal changes; but this only to the extent of 2 per cent. per degree. The degree of ionization also increases, but only extremely little, so that no change of known physical properties will explain the phenomenon. Various hypotheses which need not detain us have been put forward.

Unexplained though it may be, yet the quantitative treatment of the subject is clear enough and, I think, as cogent in the living organism as in the test-tube. If so, we may consider ourselves now justified in separating off from the realm of stimulation yet a third class of causal connection, namely, that between temperature and general intensity of vital processes.

Conclusion.

In this attempt to assert the inevitableness of the action of physical-chemical principles in the cell, I have not ventured upon even the rudiments of mathematical form, which would be required for a more precise inquiry. Biochemistry is indeed becoming added to the ever-increasing number of branches of knowledge of which Lord Bacon wrote:

> Many parts of nature can neither be invented with sufficient subtility, nor demonstrated with sufficient perspicuity, nor accommodated unto use with sufficient dexterity, without the aid and intervening of the mathematics.

In this sketch which I have had the honor of outlining before you I have critically considered but few points. I have rather endeavored to distribute imperfect data in the perspective in which they appear from the point of view of one who seeks to simplify phenomena by extending the principles of chemical mechanics as far as possible into the domain of vital metabolism. Much critical quantitative work has yet to be done before the whole becomes an intelligible picture.

To me it seems impossible to avoid regarding the fun-

damental processes of anabolism, katabolism and growth as slow chemical reactions catalytically accelerated by protoplasm and inevitably accelerated by temperature. This soon follows if we once admit that the atoms and molecules concerned possess the same essential properties during their brief sojourn in the living nexus as they do before and after.

Perhaps the more real question is rather as to the importance and significance of this point of view. Protoplasmic activity might be something so much *per se,* and the other factors of the nature of stimuli might be superposed so thickly upon that substratum which should be dominated by simple principles of chemical mechanics that for practical purposes the operations of the latter would be so overlaid and masked as to be neglible. A survey of this field, however, seems to show that this is not so, and that the broad action of the law of mass and the acceleration of reaction-velocity by temperature are obviously responsible for wide ranges of phenomena.

Now the conception at the bottom of these principles is that of reaction-velocity, and the conclusion of the whole matter is that the physiologist must frankly take over from physical chemistry this fundamental conception.[20] Under definite conditions of supply of material and temperature there is a definite reaction-velocity for a given protoplasm, and the main factors that alter the rate of metabolism, viz., heat, nutrition and traces of impurities are exactly the factors which affect the velocity of reactions *in vitro.*

Working on this basis we no longer need the vague unquantitative terminology of stimulation for the most fundamental of the observed "responses" to external con-

[20] No general treatment of the physiology of plants has yet been attempted in terms of reaction-velocity. Czapek, however, in the introduction to his stupendous Biochemie der Pflanzen, Vol. I, 1905, does draw attention to the conception of "reaction-velocity" and refers to the standard literature on this subject and on catalysis, though direct application is not made to the plant. Cohen (Physical Chemistry for Physicians and Biologists, English edition, 1903) considers in detail some biological applications of the acceleration of reactions by temperature.

ditions. Three sets of phenomena we have observed which, though usually treated in the category of stimulation, draw a clearer interpretation from the conception of reaction-velocity. These were: (1) the relation of development to the absence or deficit of single essential food constituents; (2) the occasional striking effect of minute traces of added foreign substances upon the whole rate of growth and metabolism; and (3) the general doubling of the activity of vital processes by a rise of 10° C.

The next higher stratum of principles should be the complications introduced by limiting factors which interrupt the extent of the manifestations of these principles and by various correlations, as, for example, that by which the reaction-velocity of one catabolic process might withdraw the supply of material needed for full activity of another different process. To this sort of relation may be attributed that phenomenon so characteristic of the more complex vital processes and quite unknown in the inorganic world, namely, the optimum.

Finally, superposed upon all this comes the first category of phenomena that we are content still to regard as stimulatory. From the point of view of metabolism and reaction-velocity many of these appear very trivial, though their biological importance may be immense. Think how little the tropistic curvatures of stems and roots affect our quantitative survey; yet a little rearrangement of the distribution of growth on the two sides of an organ may make the difference between success and failure, between life and death.

From our present point of view vision does not extend to the misty conceptions of stimulation upon our horizon. We may therefore postpone speculation upon the mechanical principles governing them and await the time when by scientific operations we shall have reduced to law and order the intervening region, which we may entitle the chemical substratum of life. This done we may venture to pitch our laboratory a march nearer to the phenomena of protoplasmic irritability and make direct attack upon this dominating conception, the first formidable bulwark of vital territory.

THE DESICCATION OF ROTIFERS

D. D. WHITNEY

COLD SPRING HARBOR, LONG ISLAND, N. Y.

THE general statement often found in text-books that "Adult rotifers can survive prolonged desiccation and resume active life when again placed in water," seems to have been made without sufficient warrant.

While working with the rotifer, *Asplancha brightwellii*, my attention was repeatedly called to the fact that when the water became sufficiently evaporated so as to expose only a portion of the body of the rotifer to the air it never recovered when placed again in a larger quantity of water and soon died. Doubt as to the truth of the general statement regarding desiccation naturally arose and in consequence a series of experiments were carried out to test the matter.

Forty-five species of rotifers that were collected in the various ponds and pools in the vicinity of Cold Spring Harbor, New York, were dried at room temperature, from a few hours to several days, during the months of July and August. They were dried without being exposed to direct sunlight in a hollow ground slide, upon filter paper, in sediment taken from the water in which the rotifers lived, and also in sediment mixed with sand. Masses of the water plants, Lemna, Myriophyllum and others among which many species lived were also dried. After the water seemed to have been completely evaporated fresh spring water was added and those animals that ever revived did so within ten to twenty minutes after the water was added. Drying the rotifers in masses of sediment and in sediment mixed with sand was found to lead to more recoveries.

In all experiments many species were dried in the same lot and in nearly all of them these were mixed with rotifers which were known to withstand drying. If none of

the animals revived when water was added it was assumed that the method of drying of the lot was imperfect but if, on the other hand, those animals that were known to be able to withstand drying revived, when water was added, the method of drying of the lot was deemed satisfactory. It may be possible, however, that the individuals of different species, since they vary greatly in size and form, require different methods for being successfully dried and again revived. But if revival after desiccation is of general occurrence for adult rotifers the various methods of drying used in the experiments ought to have given a fair percentage of positive results.

The individuals of some of the species were obtained in countless thousands, either in nature or in artificial cultures, others were less numerous and only a few thousand or a few hundred individuals were obtained. In a small number of species only a few individuals were found and used in the experiments.

Jennings[1] classifies the rotifers in five orders: (1) Bdelloida with two families; (2) Seisonacea with one family; (3) Rhizota with three families; (4) Ploima with eighteen families; and (5) Scirtopoda with one family.

In the experiments performed no individuals were used belonging to the order Seisonacea which contains all marine forms, nor were there used any individuals of the order Rhizota which contains all the fixed forms, Representatives were used from one family of the order Bdelloida, from fifteen families of the order Ploima, and from the one family of the order Scirtopoda. Thus the forty-five species used represented seventeen of the twenty-one families in the three orders just mentioned.

The following species were used in the experiments:

Order 1. Bdelloida.

Family 1. Philodinadæ.

Species. *Rotifer vulgaris*,[2] *R. macrurus*,[2] *Philodina roseola*,[3] *P. citrina*.[3]

Order 4. Ploima.

Suborder 1. Illoricata.

[1] AMER. NAT., Vol. XXXV, p. 725.

Family 1. Microcodontidæ.
Species. *Microcodon clavus.*[4]
Family 2. Asplanchnadæ.
Species. *Asplanchna brightwellii.*[3]
Family 3. Synchætadæ.
Species. *Synchæta tremula,*[5] *Polyarthra platyptera.*[2]
Family 4. Triarthradæ.
Species. *Triarthra longiseta.*[3]
Family 5. Hydatinadæ.
Species. *Hydatina senta.*[3]
Family 6. Notommatadæ.
Species. *Taphrocampa saundersiæ,*[4] *Notommata* ———,[5] *Copeus pachyurus,*[5] *Furcularia gracilis,*[2] *F.* ———[4] *Eosphora aurita,*[3] *Diglena* ———.[5]

Suborder 2. Loricata.
Family 1. Rattulidæ.
Species. *Mastigocerca mucosa,*[2] *M. bicornis,*[2] *M.* ———.[3]
Family 2. Dinocharidæ.
Species. *Dinocharis tetractis,*[4] *Scaridium longicaudatum,*[5] *S. endactylotum.*[5]
Family 3. Salpinadæ.
Species. *Salpina eustala.*[2]
Family 4. *Euchlanidæ.*
Species. *Euchlanis dilatata,*[5] *E. triquetra.*[4]
Family 5. Cathypnadæ.
Species. *Cathypna leontina,*[4] *Distyla gissensis,*[2] *D. stokesii,*[4] *Monostyla lunaris,*[2] *M. bulla,*[2] *M. quadridentata.*[2]
Family 6. Coluridæ.
Species. *Colurus bicuspidatus,*[5] *Metopidia lepadella,*[2] *M. triptera,*[2] *M.* ———.
Family 7. Pterodinadæ.
Species. Pterodina patina,[4] *P. reflexa.*[4]
Family 8. Branchionidæ.
Species. *Branchionus bakeri,*[5] *B. urceolaris,*[3] *B. pala,*[3] *B. angularis,*[3] *Noteus quadricornis.*[5]
Family 10. Pleosomadæ.
Species. *Pleosoma truncatum*[2] (?).

Order 5. Scirtopoda.
Family Pedalionadæ.
Species. *Pedalion mirum.*[2]

[2] Few thousand individuals used in the experiments.
[3] Many thousand individuals used in the experiments.
[4] Probably less than a hundred individuals used in the experiments.
[5] Few hundred individuals used in the experiments.

This list is far from being complete but it represents so many families of the free swimming rotifers upon which the general statement in regard to desiccation is supposedly based that the results obtained ought to indicate whether the phenomenon of desiccation is widespread among the common forms.

Philodina roseola and *Philodina citrina* were the only forms of the forty-five experimented upon which could successfully withstand desiccation and resume normal activities when again placed in water. Some of them remained ten days in small masses of débris, 1–2 mm. in diameter, which were as thoroughly dried as possible in the laboratory atmosphere. Those that were dried in the sun never revived when again placed in water. This may have been due to a too complete desiccation or to the high temperature, which was usually about 45° C.

The cuticle in the Philodinadæ is less specialized in the structure than in any of the other families of the three orders, and as this structural character is of great importance in the present system of classification the family may be considered the lowest or most primitive of all the twenty-one families. It is interesting to note, however, that some of the species of another genus, Rotifer, of the same family, can not withstand complete desiccation. In several experiments in which the four species of Philodina and Rotifer were mixed together in the débris, sediment or water plants, all four species would revive if the material in which they were contained was not completely dried, but only the two species of Philodina revived when the drying was complete. Systematists separate the two genera by the position of the eyes but evidently there is a more fundamental difference than this which means life and death in times of drought.

The common misconception regarding desiccation may probably have arisen, in part, from the fact that when mud or sediment from ponds in which rotifers live is dried living rotifers appear after a few hours when water is added to the sediment. These living rotifers prob-

ably develop however from the "winter eggs"; thick shelled fertilized eggs, which in some cases are known to withstand prolonged desiccation.

During this summer some winter eggs of *Asplanchna brightwellii* and *Hydatina senta,* which had been laid in June, were kept in water taken from the culture[6] jars until August 3. Then they were taken out with a little sediment and allowed to dry. On August 5, the sediment was apparently thoroughly dried. On August 10 spring water was added and at the end of twenty-four hours several small Asplanchna were swimming about in the water. Later young Hydatina were found in the water. The eggs seem to vary much in the length of time required for them to hatch, some not hatching for three or four days after being placed in spring water while others hatch within twenty-four hours. This may be due to differences in the rate of rapidity in which water penetrates the egg membranes. In sections of the winter eggs of *Hydatina senta* it is very noticeable that the thickness of the outer egg membrane varies greatly in different eggs.

On August 4 ten to fifteen cubic centimeters of mud and sediment were collected in a finger-bowl from the pond in which *Asplanchna brightwellii, Branchionus urceolaris*, and *Pedalion mirum*, were living and allowed to dry in the sun. The next day the mud was thoroughly dried so it would readily crumple between one's fingers. In this condition it was kept until August 10 when the finger-bowl was filled with spring water. On the following day several individuals of each of the above three species were swimming about in the water.

When ponds and pools in which rotifers live are in the process of drying up the water becomes so foul by the decomposition of dead plants and animals that all the rotifers of some species die before the pool is completely dried. If, on the other hand, rotifers are kept in the laboratory in very clean water which is allowed to slowly

[6] *Jour. Exper. Zool.*, Vol. V, p. —.

evaporate they all die, presumably of starvation. It is also interesting to note that some pools do not become dry during the summer but the rotifer fauna changes completely several times during the season. A small pond in this vicinity was teeming with *Asplanchna brightwellii* and *Branchionus urceolaris* during the early part of July but by the middle of August not an individual of either species could be found in it. Individuals of Pedalion and Polyarthra were very numerous at this time but in the latter part of August not one could be found. The pond was now teeming with *Branchionus angularis, B. pala* and *Triarthra longiseta* but no individual of the first four species named above was present.

In a case like this desiccation could play no part in the preservation of the species and they could only be saved by winter eggs.

Some winter eggs of *Asplanchna brightwellii* which were laid in June in artificial cultures were buried July 3 in an ice house upon a cake of ice where the temperature was 1–2° C. On August 7 they were removed from the ice house to ordinary room temperature and the old culture water replaced by fresh spring water. At the end of forty hours several young Asplanchna were swimming about in the water.

Many other winter eggs which were laid at the same time as the above lot but which had remained in the laboratory at room temperature in a bottle containing water, taken from the culture jar in June were placed in fresh spring water. In many cases within an hour the thick outer egg membrane had cracked open and exposed about a fourth of the thin inner membrane which surrounded the embryo. The history of some of these eggs was followed and it was found that they produced normal young animals on the following day. The swelling and cracking open of the thick outer membrane is obviously due to the sudden great change of osmotic pressure which is

brought about by removing the eggs from a somewhat foul and cencentrated culture to fresh spring water.

This process of causing winter eggs to develop in the summer is very likely the same that occurs in nature in the spring months. During the fall and winter the pools become free from abundant animal and plant forms and the accompanying products of decomposition by the frequent floodings by rains and the low temperature. In the spring the heavy rains flood the pools again and the osmotic pressure of the water is so much lower than it was in the previous summer that the eggs absorb water enought to rupture the thick outer membrane and stimulate the embryos to growth. As the temperature becomes favorable they develop and the life cycle is completed.

From the foregoing observations it seems probable that desiccation of the adult rotifers followed by revival is not of widespread occurrence in the group and is not the means resorted to by most species for tiding over unfavorable periods. Survival is due in most cases to the winter eggs which can withstand both desiccation and a low temperature.

ON THE HABITS AND THE POSE OF THE SAUROPODOUS DINOSAURS, ESPECIALLY OF DIPLODOCUS

DR. OLIVER P. HAY

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To most persons the habits of living animals are more interesting than is their anatomy. The same is probably even more true with respect to the extinct animals. However, when it comes to determining the habits of extinct animals, their aquatic or terrestrial habitat, their modes of progression, their bearing on their limbs, their food and their ways of procuring it, their modes of attack and defense against their enemies, their manner of reproduction, etc., we meet with many difficulties.

The Sauropoda, and especially the species of Diplodocus, offer a fine illustration of the difficulties mentioned. Were they aquatic, or terrestrial, or amphibious? Did they affect dry lands, or swamps, or rivers and lakes? Did they eat vegetable food or did they prey on other animals? Did they chew their food or did they bolt it? Did they bring forth living young or did they lay immense eggs? Did they make bold attacks on their enemies or were they timid and cowardly creatures? Did they walk only, or swim only, or did they employ both methods of transporting their huge bodies? If they walked, was it on all four legs or on the hinder ones only? If on all four, did they carry their bodies high above the ground, after the manner of the ox and the horse, or did they carry them low down, like the crocodiles, perhaps dragging their bellies on the ground?

To some of these questions more or less definite answers have been made and accepted; others remain unanswered. It is pretty well agreed that a part of their time was passed in the water; that they could swim

readily; that they walked mostly on all fours; that to some extent at least they went about on land; that their food was mainly, if not wholly, vegetable; and that they had imperfect or no means of chewing it.

We are assisted in understanding the habits of these creatures by a knowledge of the nature of their environment. And this we must determine from the character of the deposits in which their bones are discovered and from the kinds of animals and plants accompanying them. Investigation has shown that their remains occur in sandstones and clays which were certainly laid down in fresh waters having no great amount of motion. The accompanying animals are other dinosaurs, some herbivorous, others carnivorous; besides crocodiles, turtles, freshwater fishes and freshwater shells. Some of the plants that occur in the deposits certainly lived in fresh water.

Hatcher[1] has discussed at length the nature of the region in which the species of Diplodocus and their allies lived, as well as the habits of the Sauropoda in general; and the present writer agrees with him on most points. Hatcher believed that the Atlantosaurus beds were deposited, not in an immense freshwater lake, as held by some geologists, but over a comparatively low and level plane, which was occupied by perhaps small lakes connected by an interlacing system of river channels. The climate was warm and the region was overspread by luxuriant forests and broad savannas. The area thus occupied included large parts of the present states of Colorado, New Mexico, Utah, Montana, and the Dakotas. In his memoir on Diplodocus, Hatcher[2] compares the conditions prevailing in that region during the Upper Jurassic to those now found about the mouth of the Amazon and over some of the more elevated plains of western Brazil. In such regions the rivers, fed from distant elevated lands, must have been subject to frequent inundations.

[1] *Mem. Carnegie Mus.,* II, 1903, pp. 54–67.

[2] *Mem. Carnegie Mus.,* I, p. 60.

The beds of the streams were continually shifting, and there existed numerous abandoned channels that were filled with stagnant water. An animal that lived in such a region would be compelled to adapt itself to a more or less aquatic life, and this adaptation would be reflected to a greater or less extent in the structure of the animal. Marsh had concluded from the position of the external nares of Diplodocus that it was addicted in some measure to an aquatic existence. The feet too are of rather peculiar structure, the inner toes being strongly clawed, the outer toes greatly reduced; but the meaning of this is differently interpreted.

The Food of Diplodocus

The particular sort of food eaten by the species of Diplodocus is unknown, but nobody doubts that it was vegetable. The teeth were pencil-like in form and they were entirely confined to the front of the jaws. By general consent, they could have been employed only for prehension of food, not at all for its mastication. Hatcher suggested that the teeth might have been useful in detaching from the bottoms and shores the tender and succulent aquatic and semi-aquatic plants that must have grown there in abundance. Osborn[3] says that "the food probably consisted of some very large and nutritious species of water plant. The anterior claws may have been used in uprooting such plants. . . . The plants may have been drawn down the throat in large quantities without mastication." In a restoration of Diplodocus by Mr. Charles W. Knight[4] the animal is represented as standing on its hind legs and preparing to bite off the terminal bud of a towering cycad. Holland[5] thinks that the teeth were better adapted for raking and tearing off from the rocks soft masses of clinging algæ than for securing any other forms of vegetable food now represented in the waters of the world.

[3] *Mem. Amer. Mus. Nat. Hist.*, I, p. 214.

[4] *Scientific American*, XCVI, 1907, p. 485.

[5] *Mem. Carnegie Mus.*, II, p. 240.

To the present writer the suggestion of Dr. Holland has in it more of probability than any of the others presented. If the food-plants sought by Diplodocus had been large and such as required uprooting by the great claws of the reptile the prehension and manipulation of the masses would have been liable to break the slender teeth and would certainly have produced on them perceptible wear. The upper teeth of the original of Marsh's figures on Plate XXV of the Dinosaurs of North America[6] show no wear, so far as the writer can determine. The mandibular teeth are not well exposed to view.

With respect to Osborn's theory, it is well to take into consideration also the probable ability of the reptile to digest great masses of undivided and unmasticated vegetation. Against the theory suggested by Knight's restoration it may be urged that the teeth, pointed or slightly chisel-shaped, are poorly adapted for cropping leaves and great buds; most of all, the teeth have spaces between them, like the teeth of a great comb, an arrangement not favorable to their functioning as cutting instruments. The teeth could hardly have been used for scraping algæ from rocks, either, for that usage would have produced evident and rapid wear. It is more probable that the food consisted of floating algæ and of plants that were loosely attached to the bottoms of stagnant bayous and ponds. Hatcher has reported[7] the finding of the seeds and the stems of a species of Chara near the Marsh quarry, where many Sauropoda have been found. This alga, it seems to the writer, would have been admirably adapted to the needs of Diplodocus. It could be easily gathered into the mouth as the reptile swam or crawled lazily about or rested itself and retracted and extended its long neck. The long and highly vaulted palate would have permitted a considerable mass to be collected, out of which, by pressure of the tongue, the superfluous water might have been squeezed between

[6] (Cat. No. 2672, U. S. Nat. Mus.)

[7] *Mem. Carnegie Mus.*, II, p. 63.

the spaced teeth. In addition to various algæ there were probably other floating plants.

THE POSTURE OF DIPLODOCUS

Marsh presented no restoration of Diplodocus, but he did furnish restorations of Brontosaurus; and he stated that he regarded it as representing the general form and proportions of the Sauropoda. In this figure Brontosaurus is shown as walking with the body high above the ground and with the limbs, especially the hinder ones, about as straight as they are in the elephant.

So far as the bearing of Brontosaurus and Diplodocus on their limbs is concerned, Marsh's example has been almost slavishly followed ever since. No one, so far as the writer knows, has ventured to defend in print a more crocodilian posture. Osborn[8] grants that there is room for wide differences of opinion as regards the habits and means of locomotion of these gigantic animals and states that some hold the opinion that on land at least these reptiles had rather the attitude of the alligator. The same writer says in *Nature*, vol. 73, 1906, p. 283, that Dr. Matthew and Mr. Gidley have maintained the latter view. However, the trend of opinion seems to have been in the opposite direction. Osborn[9] suggested that Diplodocus might lift its fore limbs from the ground and support itself on the hinder legs and the tail. This idea has found expression in Knight's restoration referred to above. Osborn's general notion of Diplodocus seems, however, to be that it was essentially an aquatic animal, long, light-limbed, and agile, and capable of swimming rapidly by means of its great tail, provided, as he thought, with a vertical fin; yet occasionally going about on land. Hatcher[10] opposed the view that Diplodocus was aquatic; and he showed that there is no evidence of the presence of a vertical fin. The compression of the

[8] *Science*, XXII, 1905, p. 376.

[9] *Mem. Amer. Mus. Nat. Hist.*, I, p. 213.

[10] *Mem. Carnegie Mus.*, II, 1903, p. 59.

centra where the fin is supposed to have been situated seems to have been slight, and the neural spines are not higher than elsewhere. The present writer finds neither in the feet nor in the tail any special arrangements for swimming. For navigation in its restricted waters no fin was needed. Almost any colubrid snake makes fair progress in the water, notwithstanding the absence both of a compressed tail and of a vertical fin.

Hatcher's final view does not, after all, appear to have been greatly different from that of Osborn. He held that Diplodocus, as well as most of the Sauropoda, were essentially terrestrial animals, but that they passed much, perhaps most, of their time in shallow water, where they could wade about and search for food. He believed that they were ambulatory, but quite capable of swimming. Hatcher's language does not necessarily imply that these animals walked about after the fashion of quadrupedal mammals, but his restorations show plainly that such was his conception.

This conception has prevailed in the plaster reproductions of the skeleton of Diplodocus which have been sent abroad by the Carnegie Museum and set up in London, Berlin and Paris; and in the small plaster restorations issued by the American Museum of Natural History. However, the limit of quadrupedal erectness, rigidity, rectangularity, and rectilinearity has quite been reached in the skeleton sent by the last mentioned institution to the Senckenberg Museum, at Frankfort-on-the-Main. In this case the poor beast is made to stand straight-legged and almost on the tips of its digits. On the other hand, the American Museum's skeleton of Brontosaurus, a much larger and heavier reptile and one sorely needing the mechanical advantage of straight legs, in case it had to bear its body free from the ground, has been presented to the modern world as having been decidedly bow-legged.

To the present writer it appears that the mammal-like pose attributed to the Sauropoda is one that is not required by their anatomy and one that is improbable.

The current conception is one that is easily accounted for. Before exact knowledge of these reptiles had been gained, it was known that the dinosaurs of the other groups, herbivorous and carnivorous, walked erect, after the manner of birds. It was indeed necessary, on account of the length of the fore limbs, to place the Sauropoda on all four feet; but analogy caused it to be supposed that the limbs were disposed, with reference to the vertical plane of the body, similarly to those of the bipedal dinosaurs. The conception of a creeping dinosaur was hardly to be entertained. The straight femora of these reptiles, having the head and the great trochanter moderately developed, lent probability to the idea.

If the straightness of the femora is relied on to support the correctness of the prevailing restorations of the Sauropoda we may call attention to the equally straight femora of sphenodon and of the lizards. Notwithstanding the great size of the carnivorous dinosaur Allosaurus and the fact that the whole weight of its body was commonly borne by the hinder limbs alone, its femora are considerably bent. The prominence and the height of the great trochanter of the Sauropoda do not appear to be such as to have prevented the femora from standing out at right angles with the body. Both the head of the femur and the acetabulum were doubtless invested with much cartilage, so that we can not now be wholly certain about their form and fitting. The same may be said regarding certain other articulations of the limbs. Hatcher[11] has spoken of the character of the articulations and he has expressed the opinion that the habitual support of the body in the air could not have failed to produce closely applied and well-finished articulations, and Osborn had previously expressed the same idea.[12] There is indeed a great difference between the articulations of the limbs of the Sauropoda and those of the Theropoda, such as Allosaurus and Ceratosaurus.

[11] *Mem. Carnegie Mus.*, I, p. 59.

[12] *Bull. Amer. Mus. Nat. Hist.*, X, p. 220.

Osborn[13] has found in the large preacetabular process an argument in favor of the ability of Diplodocus to elevate the anterior part of its body. However, Trachodon, which habitually walked on its hind legs has a very insignificent preacetabular process. The crocodiles have a strongly developed process in front of the acetabulum.

It appears to the writer that the structure of the feet of the Sauropoda indicates that the digits were directed somewhat outward, instead of directly forward, as they are placed in the restorations. The strongly developed inner digits would then have come more effectively into contact with the ground than the much reduced outer digits and would have been employed by the animal as a means of pushing itself along. In case the lower end of the radius is placed in front of the ulna, as represented by Hatcher [14] it appears probable that the foot would be directed more strongly outward than is shown in his restoration.[15]

The writer is not aware that any one has held that the Sauropoda could not, at least while resting, assume a crocodile-like posture, with the abdomen on the ground and the limbs extended outward on each side. If such a position is admitted as possible, the arguments derived from the anatomy in favor of an erect mode of walking are greatly weakened. If such a pose was not assumed, what was the pose? Did Diplodocus and Brontosaurus lie down on their sides, as an ox or a horse does when sleeping? Or did they lie prone, with the limbs drawn up under them, as a dog sometimes does? These positions appear to be improbable. It is worth considering too what disposition Diplodocus made of its elephantine legs while it was swimming with the agility that has been imputed to it.

The weight of Diplodocus and of Brontosaurus furnishes a strong argument against their having had a

[13] *Mem. Amer. Mus. Nat. Hist.*, I, p. 210.

[14] *Mem. Carnegie Mus.*, II, p. 73, Fig. 1.

[15] *Op. cit.*, Pl. VI.

mammal-like carriage. There will be little dissent from the view that these animals inhabited a country in which marshy lands abounded and that they passed the most of their time in the vicinity of bodies of water. As to weight, Marsh estimated that that of Brontosaurus was more than twenty tons. Each footprint was thought to be about a square yard in extent. The pressure was therefore about 1,100 pounds on each square foot of the ground. What progress could such enormous animals have made through morasses and along mud-depositing rivers, in case they carried themselves as they are represented in the restorations? Without doubt, they would soon have become inextricably mired and would have perished miserably.

Osborn[16] has suggested that Camarasaurus, another sauropod was accustomed to wading about in rivers where the bottoms were sandy and firm. The habits of Diplodocus could have differed little from those of Camarasaurus. It is difficult to understand why an animal whose immediate ancestors must have walked about in a crocodile-like manner, an animal that was stupid and probably slow of movement, an animal which could by means of its long neck reach up from the bottom many feet to the surface and from the surface many feet to the bottom—why such a reptile should need to develop the ability to walk along river bottoms like a mammal. Furthermore, it seems somewhat overgenerous to impute to a reptile so many and so diverse activities as swimming with great facility, walking on river bottoms and on the land with mammal-like gait, and on occasion erecting itself on its hinder legs after the manner of a bird, in order to crop the foliage from the tops of high trees, when this reptile was sixty feet long, weighed many tons, had a brain little larger than one's two thumbs placed side by side, and was provided with a feeble dental apparatus with which to gather food wherewith to support its huge body, and that food of a sort that yielded little energy in proportion to its bulk.

[16] *Bull. Amer. Mus. Nat. Hist.*, X, p. 220.

The writer's conception of Diplodocus is that it was eminently amphibious, that it could swim with considerable ease, and that it could creep about on land, with perhaps laborious effort. When feeding it must have swam or crept lazily about, gathering in floating plants and such as were attached loosely to the bottom. If any plants that were relished grew at some depth they could be reached by the long neck; or, if there was foliage twenty feet above the water it could be as easily gathered in. That a Diplodocus ever stood on its hind lgs is hardly more probable than that crocodiles may perform the same feat.

The large size of Diplodocus does not preclude the possibility that it could creep about on the land. *Crocodylus robustus,* of Madagascar, is said to attain a length of 10 meters, and yet it doubtless is able to walk as other crocodiles walk. The limb bones of Diplodocus and of Brontosaurus are proportionally as large as those of crocodiles.

It seems to the writer that our museums which are engaged in making mounts and restorations of the great Sauropoda have missed an opportunity to construct some striking presentations of these reptiles that would be truer to nature. The body placed in a crocodile-like attitude would be little, if any, less, imposing than when erect; while the long neck, as flexible as that of an ostrich, might be placed in a variety of graceful positions.

SHORTER ARTICLES AND CORRESPONDENCE

JUVENILE SUBSTITUTES FOR SMOKING TOBACCO

Nearly every boy has the desire to smoke and while many perhaps begin with tobacco itself, many more probably experiment with other substances of vegetable origin which burn well and yield readily the desired smoke so that the appearances, at least, of the act of smoking are produced. The knowledge of such substitutes in a particular locality is usually extensive and widespread, being the subject of serious conference and debate among the youthful inhabitants. Very little, if any, of this tradition is recorded, and it seems perhaps a matter of some botanical interest that it should be. In some ways, the practise of boys in thus providing a substitute bears a singular resemblance to that of the less civilized peoples or communities more or less isolated from tobacco-producing centers.

My own juvenile knowledge was obtained in eastern Connecticut between thirty and forty years ago. In those days there were still many umbrellas with rattan (*Calamus rotang?*) ribs. Short pieces of these, being porous, on being set afire at one end, a matter of some difficulty, allowed the smoke to be drawn through in sufficient quantities to be blown out through the mouth, but the smoke was hot and biting and the rattan was kept alight with difficulty. Later, I learned the virtues of the more generally used substitutes, hay-seed, sweet-fern and mullein. The hay-seed was usually procured from the floors of the hay barns and consisted of the more or less ripened florets of timothy (*Phleum pratense*) and redtop (Agrostis sp.) It was usually more or less carefully sifted and smoked in a clay pipe or packed in paper shells to imitate cigarettes. This was before the days of the universal use of hand-rolled cigarettes and no such papers were available, so we used a fairly stiff white paper, rolled it about a cylindrical piece of wood of desired length and diameter, fastening the free edge by means of home-made starch paste. When these were dry, they were carefully stuffed with the hay-seed and the ends carefully, if not skilfully, folded in. Very commonly, however, the ends came undone during the smoking and the fine hay-seed made a disagreeable mouthful. A more

popular filling consisted of the leaves of the sweet-fern (*Myrica asplenifolia*). The leaves were selected when green and fragrant, carefully dried in the sun or in the oven, until brittle, then thoroughly pulverized by rubbing between the hands, and finally sifted through a coarse sieve. This was then packed tight in cigarette shells, and sweet-fern cigarettes required some skill. The making of high-grade cigarettes of this kind was one of my specialties, and one summer I drove a thriving trade in them, disposing of a considerable number at the remunerative price of ten for one cent. The lower leaves of the common mullein (*Verbascum Thapsus*) were gathered chiefly as they were found dried on the plant, roughly pulverized and smoked in a clay pipe. They were supposed to closely resemble real tobacco and were the preparatory stage to genuine smoking. Often some small boy was inveigled into smoking fine-cut tobacco of the "Durham" or "Lone Jack" type under the impression that he was simply indulging in a pipe of mullein. The resulting sickness, as a rule, undeceived him and he realized too late that he had been made the victim of a joke more practical than pleasant.

For the long-cut tobacco, we found a fair substitute, at least in appearance, in the brown and dried ends of corn silk, but it was never so very popular with us. I have found on questioning, that these same substitutes were known to the generation preceding mine and that they are equally well known to the generations coming on to fill our places. I have also learned of other substitutes not known to us as well as a widespread knowledge of some of those mentioned.

I find that there is a widespread use of tea and ground coffee for pipe smoking, and some use even of ground cinnamon. The older youth often take to cubebs, following the officinal use of the same. A use seems also to be made of the porous internodes of the grape-vine, as we used rattan, and even of tightly rolled tubes of cinnamon stick. I have also been told that some boys roll paper about the sticks of "punk" used to touch off fire crackers on the Fourth of July, and light and smoke them.

Inquiring of the boys in California, I find that they use corn silk and various leaves for pipe smoking. The leaves of maple, grape, fig, rose and willow are commonly employed. Perhaps the most popular of all are the leaves of the worm-wood (*Artemisia heterophylla*) which is common on most hillsides and gives a pleasing aromatic smoke. In many places, the old fallen leaves

of the blue gum (*Eucalyptus globulus*) is a favorite. The leaves of yerba santa (*Eriodictyon californicum*) is smoked to cure colds and also by the boys for the pure joy of smoking. The leaves of the California bay (*Umbellularia californica*) are often used in the same ways. I am informed by Dr. H. M. Hall that the composite *Atrichoseris platyphylla* is called "Tobacco weed" by the boys of Palo Verde, in the Colorado Desert of California and is in decided favor with them for smoking. This plant is decidedly rare to the botanist, but after heavy rains it becomes plentiful in sandy places and its broad basal leaves are well adapted to being rolled into "cigars."

Dr. G. H. Shull informs me that the leaves of the American pennyroyal (*Hedeoma pulegioides*) is smoked by the boys in some parts of Ohio.

The wild species of Nicotiana have furnished and still do furnish the smoking materials of certain aboriginal peoples from the neighborhood of Oregon south to Chile, but there is no record of their having been used by juveniles of the white races. I learn, however, from Professor R. H. Forbes, of the University of Arizona, that the "wild tobacco" of the neighborhood of Tucson, which, however, is *Nicotiana glauca*, the tree tobacco, is smoked by boys and without injurious effect.

The above facts are probably but a few of those on this subject which may be gathered and I trust that others may take sufficient interest to add to the list.

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NOTES AND LITERATURE

HEREDITY

Recent Studies in Human Heredity.—Must the fallacy always persist that all ancient and powerful families are necessarily degenerate? As long ago as 1881, Paul Jacoby wrote a book[1] to prove that the assumption of rank and power has always been followed by mental and physical deteriorations ending in sterility and the extinction of the race. By collecting together all evidence supporting his preconceived theory, by tracing only the well-known families in which pathological conditions were hereditary, by failing to treat of dozens of others whose records would not have supported his thesis, by saying everything he possibly could that was bad about every one (following always the hostile historians), by ignoring everywhere the normal and virtuous members, he was able to present what was to the uninformed an apparently overwhelming array of proof. In regard to the injustice of this one-sided picture I have already had something to say in "Mental and Moral Heredity in Royalty,"[2] first published some six years ago.

A further study based upon Jacoby's unsound foundations has recently come to my notice,[3] and although a well-made book containing an interesting series of 278 portrait illustrations, is necessarily quite as misleading as the older structure on which it rests. The main idea of Dr. Galippe is to show that the great swollen protruding underlip which descended among the Hapsburgs of Austria, Spain and allied houses, and also the protruding underjaw (*prognathisme inférieur*), are stigmata of degeneracy, and to demonstrate this he places beside his portraits, quotations from the writings of Jacoby.

Galippe uses no statistical methods, not even arithmetical counting, and appears to be totally ignorant of English biometric writings. His general conclusions about the causes of degeneracy (aristocratic environment, etc.) are quite as mis-

[1] Etudes sur la sélection chez l'homme. Paris, 1881, 2d ed., 1904.

[2] *Popular Science Monthly*, August, 1902–April, 1903. Also extended in book form, New York, Holt, 1906.

[3] V. Galippe. L'hérédité des stigmates de dégénérescence et les familles souveraines. Paris, 1905.

leading and unfounded as those of Jacoby, and I fear he could not even prove that the anatomical peculiarities are really stigmata of degeneration at all.

If abnormal mouths, noses and ears are to be proved the stigmata of degenerate or criminal types it is necessary to prove by biometrical methods, a correlation between the bodily anomalies on one hand, and the existence of psychic defect on the other. Galippe does not attempt to show such a correlation.

I have taken all the cases available, and divided Galippe's portraits into three classes, those in which the "lip" is "marked," those in which it is "slight" and those in which it is "absent." I have tried correlating these 205 cases with the mental and moral grades which I had previously obtained for these individuals; but I find that any correlation must be slight and difficult to prove without much larger data. For instance, of the distinctly inferior individuals 25 show the "lip" in a "marked" degree, against 20 in whom it is "absent"; while of the notably superior persons 22 have the "marked lip" against 21 in whom it is "absent." It may be similar to the slight correlation that is now thought to probably exist between genius and insanity. But this is not like saying that genius is insanity.

Many of Galippe's portraits labeled *"Prognathisme inférieur"* strike the reader as showing nothing peculiar in any way, others nothing more than a heavy underjaw, a common characteristic of the old royal personages, which so far from being a sign of degeneracy may as likely be associated with their general strength of character and determination of will.

But the most misleading side of Galippe's work, in which he also follows Jacoby, is his constant repetition of the word sterility and his frequent statements that noble and illustrious families thus find their natural end. The chief cause of this common mistake has arisen from following down, from ancient times to the more recent, the various dynasties in the male lines of primogeniture. In an appendix to Galton's "Natural Inheritance," 1889, this question is discussed, and it is there shown that *all* male lines, including the surnames of commoners, tend to diminish merely from the law of chance. This is because whenever all girls are born in any branch the name is lost absolutely, and can never be recovered. If the daughters marry and have children, the germ plasm is still transmitted, though

the name is no longer the same. The old dynasties, Plantagenet, Stuart, Romanoff, Vasa, etc., have become extinct in one sense, although not in another. If certain royal families have gone, what is to be said with regard to the following facts.

The male lines of all the present reigning families of Europe are carefully traced in the *opposite* direction, that is back to their earliest noble ancestors, in a most carefully compiled book by Dr. Kamil von Behr.[4]

With the exception of the present reigning family of Sweden, all have been princes, counts or dukes far into the remote past. These show from 20 to 33 generations of noble blood, in the direct male lines. The following is a list of the present royal families with the earliest authentic dates of their nobility. Anhalt 1059 A. D., Austria (Lorraine) 940 A. D., Baden 962 A. D., Bavaria 829 A. D., Belgium 1009 A. D., Denmark 1088 A. D., Great Britain 1009 A. D., Greece 1088 A. D., Hesse-Cassel 846 A. D., Hesse-Darmstadt 846 A. D., Italy (Savoy) 959 A. D., Liechtenstein 1133 A. D., Mecklenburg-Schwerin 960 A. D., Mecklenburg-Strelitz 960 A. D., Netherlands 992 A. D., Norway 1088 A. D., Portugal 1009 A. D., Prussia 1061 A. D., Reuss 1122 A. D., Rumania 1009 A. D., Russia 1088 A. D., Saxe-Coburg-Gotha 1009 A. D., Saxony 1009 A. D., Schaumburg-Lippe 1121 A. D., Schwarzburg 1114 A. D., Spain 861 A. D., Sweden 1810 A. D., Waldeck 940 A. D., Würtemberg 1110 A. D. When one considers that they married practically always within their own ranks, one can easily see that the present reigning families are descended from thousands upon thousands of counts, dukes, princes, kings and emperors. That all this blue blood has not produced sterility is easily seen by a glance at the "Almanach de Gotha" or any of the books containing lists of the many children who have recently been born to royal families.

It is my own belief that much of the causation underlying historical records may be elucidated by the statistical method, if all cases for or against a certain theory be impartially recorded, and then even a simple arithmetical count be taken. The higher statistical methods (biometrical) may be useful for further refinement, but even the most simple rules of arithmetic would prevent one going quite as far astray from the truth as Jacoby and Galippe have done in their one-sided and utterly unjust arraignment of royal families. It is like picturing all million-

[4] Genealogie der in Europa regierenden Fürstenhäuser. 2d ed., Leipzig, 1870.

aires corrupt and dishonorable. Truly these slanderers of royalty, because they have a certain scientific affiliation, are all the more to be dreaded; furthermore, they cast discredit on the whole hope of any elucidation of history along biological lines.

In contrast to books of this sort, one gladly takes up several recent memoirs emanating from University College, London. In the first of the publications of the new Eugenics Laboratory, E. Schuster and Miss Elderton,[5] to obtain data bearing on the inheritance of ability, have made a statistical study of Oxford class lists and of the schools of Harrow and Charterhouse. By analyzing the academic standing of different members of the same family, they show that the resemblance between father and son is represented approximately by the coefficient $r = .30$, in all their tables. The various coefficients for fraternal resemblance, range around $r = .40$. They are perfectly in accordance with the theoretical expectancy propounded by Galton for his law of ancestral heredity. They are also in accordance with the correlations found in "Heredity and Royalty."

Other coefficients found by Pearson and his students for various physical and psychical measurements are higher than these, ranging around .40 to .50 for parental and .50 to .60 for fraternal correlation. In an appendix to this memoir of Schuster and Elderton, Pearson takes up the question of the size of the coefficients and shows that the class lists of Oxford, Harrow and Charterhouse represent probably a selected group, in point of ability, in which case their variability would be reduced and also the correlation coefficients. After making for this a reasonable, though rough, correction he concludes that the coefficients of Schuster and Elderton are in close accord with those heretofore found by this same school of investigators.

David Heron[6] from the same laboratory contributes a first study of the inheritance of the insane diathesis. It is indeed a "First Study" in more senses than one, for not only is it the first work on this question from the Eugenics Laboratory, but it is not too much to say that it is the first attempt to treat the whole subject in an exact and satisfactory manner from the

[5] *Eugenics Laboratory Memoirs.* I, The Inheritance of Ability. By Edgar Schuster, M.A., and Ethel M. Elderton. London, Dulau and Co., Soho Square, W., 1907.

[6] *Eugenics Laboratory Memoirs.* II, A First Study of the Statistics of Insanity and the Inheritance of the Insane Diathesis. By David Heron, M.A., London, Dulau and Co., Soho Square, W., 1907.

statistical standpoint. Heron, on this point, makes the following just and timely complaint.

A careful examination of the annual Reports of the Asylums of Great Britain and Ireland has led to the conviction that no data at present published would enable the statistician to reach any quantitative results as to the inheritance of any single form of brain disease. Even medical treatises as a rule go no further than stating the percentage of cases in which insanity or some other want of mental balance has been recorded in the family history. As long as we do not know the total number in each class of relatives of the insane person and the exact brain defect from which they have suffered; as long as we do not know the total number of relatives of a random sample of the sane population and the exact forms of neurosis or brain disease from which they too have suffered, any attempt at a full treatment of the "inheritance of insanity" is from the statistical standpoint idle. What advantage can possibly arise from telling us that an insane person has so many alcoholic uncles if we do not know either the total number of his parents brothers and sisters, or the percentage of alcoholic members in the same grade of relationship of a sane individual of the same social class? . . . The solution of this difficulty, and the present writer believes of many other difficulties in the statistics of insanity, is to establish a General Register of the Insane for preservation in the office of the Lunacy Commissioners.

Heron's own work is based upon an analysis of 331 family trees provided by Dr. A. R. Urquhart, physician superintendent of the James Murray's Royal Asylum, Perth, Scotland. The coefficient of parental inheritance is found to be about $r = .50$ and fraternal resemblance $r = .45 - .55$. These are in close accord with other physical and mental measurements. The author is obliged to make several assumptions in regard to the general population in order to complete his calculations, so that his figures must be regarded as only a first approximation. The work is certainly in the right direction and it is to be hoped that all alienists will carefully read this valuable memoir.

Miss Elderton and Pearson[7] have published a measure of the resemblance of first cousins, especially in such characteristics as general health, intelligence, success, temper, temperament (reserved or expressive, sympathetic or callous, excitable or calm). Their correlation coefficients are not very uniform, but they show clearly enough a high degree of cousin resemblance, r

[7] Eugenics Laboratory Memoirs. IV, On the Measure of the Resemblance of First Cousins. By Ethel M. Elderton, assisted by Karl Pearson London, Dulau and Co., Soho Square, W., 1907.

ranging around .27. The results are taken from Pearson's "Family Records" and there is something in the method which would seem to artificially increase the apparent resemblance. Different people have been asked to give their opinions about cousins whom they may happen to know. Some judges would naturally be more generous than others in their estimates. It is easy to see that, by cynicism on the one hand, and optimism on the other, many cousins would be taken in pairs out of the medium groups, where they very likely belong, and where they would lower the correlation coefficient, and placed in pairs either above or below the mean, where they would improperly raise the coefficients. Actual bodily measurements would not be susceptible of error from this source and these physical measurements they have attempted to obtain. So far, the latter records are insufficient for full publication, but as far as they go they show roughly a very high value for the coefficient *r*.

The authors "conclude accordingly, from the present results, that for the purposes of eugenics, cousins must be classed as equally important with uncles and aunts, and that they may eventually turn out to be as important as grandparents." One suggestion is that any scientific marriage enactments would equally allow or equally forbid marriage between first cousins, as between grandparents and grandchild, uncle and niece, or aunt and nephew.

One of their conclusions regarding alternate inheritance confirms my own general contention of alternate inheritance in mental and moral traits, a fact on which I laid so much stress in tracing the pedigree of all the royal families. They state that "a determinantal theory of heredity, emphasizing alternate inheritance, must take precedence of any theory of simple blending for the bulk of the characters here dealt with."

The next two memoirs to which I shall make reference,[8] are especially important and timely, owing to the wide-spread prevalence of the idea that tuberculosis is an infectious disease and not especially hereditary. I have even seen it printed in large

[8] Drapers' Company Research Memoirs, Studies in National Deterioration. II, A First Study of the Statistics of Pulmonary Tuberculosis. By Karl Pearson, F.R.S. Dulau and Co., London, 1907. Drapers' Company Research Memoirs. III, A Second Study of the Statistics of Pulmonary Tuberculosis: Marital Infection. By the late Ernest G. Pope. Adirondack Cottage Sanitarium, Saranac Lake, N. Y. Edited and revised by Karl Pearson, F.R.S., with an appendix on assortative mating from data reduced by Ethel M. Elderton. Dulau and Co., London, 1908.

type in publications emanating from public health leagues that "Tuberculosis Is Not Hereditary." I do not know on what scientific basis such a dogma rests.

Professor Pearson has found cogent proof in the first of these studies that the phthisical diathesis is just as hereditary as any human characteristic we know about. It would take too much space to completely review this paper. In a few words it may be enough to say that he does not jump at the conclusion that correlation coefficients necessarily show heredity. The question of infection through members of the same family living in close contact is discussed at length; but the analysis reveals no evidence that direct infection is in any way important, as compared to the heritable diathesis.

For instance, in his second paper on this same subject he finds that if a husband is tubercular, then there is a probability that the wife will also be found tuberculous, and *vice versa*, but this correlation is not nearly so high as that between brothers and brothers, sisters and sisters, and brothers and sisters. Yet opportunities for direct infection in the case of husband and wife are of course vastly greater than among brothers and brothers, etc., who by the time of the average age of onset of the disease (twenty to thirty years) have already ceased to live in the same households.

The question of assortative mating comes in to explain a certain amount of this observed correlation between husband and wife. Assortative mating is a convenient name for the tendency of like to mate with like, aside from any question as to what causes may bring about the similarity in question. It is a popular belief that tall men marry short women, and blonds are attracted by brunettes, but the truth of the matter seems to be quite the reverse. In nine series of physical characteristics the correlations of resemblance between husband and wife have been found to range between $r = .20$ and $r = .28$. For physical characteristics nine series show a range between $r = .11$ and $r = .48$, with an average of $r = .24$.[9] The correlation coefficient for insanity between husband and wife is $r = .30$.

"Unless, therefore, any characteristics show a relationship between husband and wife markedly greater than .20 to .25 it would be very

[9] "Second Study of the Statistics of Pulmonary Tuberculosis," cited above, p. 22.

difficult to assert that this resemblance is due to other causes than those assortative processes which have just been shown to produce quite a sensible degree of resemblance in husband and wife."

Pearson is "prepared to accept with some reservation a sensible but probably not very large infective action from the available statistics of pulmonary tuberculosis." The question of assortative mating is an important one, and a knowledge of the amount to be allowed under various circumstances seems to me to be a necessary adjunct for recorrecting all the correlation coefficients of heredity which have so far been obtained by the London workers. Their coefficients agree fairly well, but they are all distinctly higher than the theoretical—fraternal are about .50 to .60 instead of the theoretical .40; paternal .40 to .50, the theoretical being .30; and so with the most remote relationships, especially the first cousin resemblances.

It is evident that if assortative mating be in general the strong force that Pearson has shown it to be, then it must in most investigations raise the correlation coefficients for heredity. To make this clear—tall fathers have on the average tall sons, though their average height is less than that of the fathers, due to the principle of regression, but now if it happens that all the tall fathers have tall wives, then the sons will get an added height from the influence of the tall mothers and will seem to resemble their fathers more than they do from the real paternal influence alone.

Among royal families assortative mating is a disturbing factor is at a minimum, for here the marriages are so often arranged by others than the parties most concerned, or are the result of some important state policy, that the question of individual selection is nearly, though I believe not quite, eliminated. This may be the reason why the coefficients for heredity found in the study of royalty are so much nearer the theoretical.

It may be well, in closing, to say a word about the general question of correlation coefficients as affording a proof of the influence of pure heredity. It may be asked—do the coefficients really prove anything more than a general resemblance between relatives? May this not be due to heredity in some cases and to environment in others, or a combination of both, in most cases? Personally I do not feel that the coefficients alone afford all the desired proof. Analysis of the material, separating the cases into classes in which environment has had greater or less time

to act,[10] or into classes which are known to have lived in different environments, or comparing contrasted children within the same family, with contrasts in the ancestry of these (alternate inheritance) or other schemes which seek to find measurable influence of the environment factor, are, some or all, necessary for any final proof.

What the correlation coefficients *do* show is this, that if heredity be the great preponderating force, creating individual differences between man and man, the coefficients that have been found are in substantial agreement with what they should be.

Further refinement is wanted, especially as to the effect of assortative mating, and the shape of the curve of distribution for psychic characters, when selected classes are taken.

Mendel's laws, so important to the horticulturists, and to the breeder of superficial traits in fancy strains of domesticated animals, has not been shown to have any bearing on human heredity, at least as concerns important characteristics.[11] The general rough principle of alternate inheritance in human heredity, leads, however, to the hope that a further study of this question may bring out certain "unit characters," more or less marked, so that here in the end there may be harmony between the two unfriendly schools, the Mendelian and the Biometrical.

F. A. Woods.

ORNITHOLOGY

Riddle on the Cause of the Production of "Down" and other Down-like Structures in the Plumages of Birds.[1]—A connection is here traced between the rate of growth and the character of the

[10] This method is employed by E. L. Thorndike in his excellent study of the "Measurement of Twins." *Arch. of Philos., Psychol. and Scientific Methods*, No. 1, New York, 1905. Also in some of the University College, London memoirs.

[11] It has been claimed to govern the inheritance of certain rare anomalies, albinism, abnormal hands, etc., also eye color (C. B. and G. C. Davenport, *Science*, Vol. XXVI, p. 589) and facial peculiarities of Red Indians when crossed with the Scotch (G. P. Mudge, *Nature*, November 7, 1907).

[1] Riddle, Oscar. The Cause of the Production of "Down" and other Down-like Structures in the Plumages of Birds. *Biological Bulletin*, Vol. XIV., No. 3, February, 1908, pp. 163–176.

structure in feathers. In a former paper[2] the same author showed that a feather is made up of a series of faint "fundamental bars," due to the manner of deposition of the feather substance. These bars are somewhat analogous to the annual rings of growth in the trunk of a deciduous tree, the tree rings showing the amount of annual increase in the tree trunk, while the bars mark the daily growth in the production of the feather. The demarkation of the fundamental bars is due to the period of reduced blood-pressure during the early morning hours (1–6 A.M.) of each day during the growth of the feather, and the defective transverse lines to malnutrition, or to reduced nutrition. As shown by Jones,[3] the nestling down or neossoptile is not a distinct and complete feather growth, but merely an apical segment of the first definitive feather, the first down being "the plumulaceous tip of the first definitive feather." The constriction between the two parts Riddle considers to be another variety of this same defect, due to insufficient nutrition. At the time of the hatching of the egg the down portion of the down feather is completed, and the shaft portion immediately succeeds, at a time when the whole source of food-supply is changed, and assimilation impaired by the intervention of a new source of alimentation. While this is obvious, experiments have been conducted to show the effects of underfeeding at the critical stage in the bird's life, and it has been found that a bird in the downy condition can thus be made to wear its downy plumage for months after it should have given place to the definitive feathers. "The 'quill' region is a part of the feather which 'normally' *almost* refuses to grow; by reducing the food-supply during and after its formation further growth may be absolutely inhibited or stopped."

From the experiments here related, the author concludes that the down portion of feathers is due to poor nutritive conditions, and that "The formation of the quill is probably the direct result of a progressive diminution of an already lessened food-supply."

Apparently all this bears upon the "how" rather than the "why" of feather production and feather structure, and is not to be given a too-sweeping application. In other words, that in the development of a pennaceous feather, the formation of its different parts—the pennaceous, the downy, and the quill por-

[2] A Study of Fundamental Bars in Feathers. *Biol. Bull.*, Vol. XII, February, 1907, pp. 165–174. Noticed in *The Auk*, January, 1908, p. 98.

tions—is not to be ascribed to the varying conditions of nutrition of the individual during the growth of a particular feather. While we would accept the hypothesis that varying blood-pressure during the twenty-four hours may give rise to the phenomena of "fundamental bars" and "defective lines," that defective areas may result from malnutrition, and that underfeeding may retard feather development, we can hardly conceive that we have here a full explanation of the differentiation of a feather into pennaceous, downy, and quill portions, or that the widely differing plumage structure shown by owls, pigeons and hummingbirds is merely a matter of nutrition, in its ordinarily accepted sense. In a moulting bird, for example, there may be hundreds of feathers in process of growth at the same time, and feathers in all possible stages of development. If reduced nutrition is necessary for the formation of the downy portions of the feather, and still further reduction of nutrition for the formation of the quill, how can all of these processes of feather growth take place, through experiment or otherwise, *in the same individual at the same time,* as we know is the case in an actively moulting bird? Each feather has its definite function, and its predestined form and character, in accordance with its position on the bird's body; and feathers differ in character in different birds in accordance with their rôle in nature, depending upon whether they are owls, or swifts, or pigeons, or penguins, etc. Evidently the nutrition of the single feather and the nutrition of the individual bird are not necessarily one and the same thing; while defective or insufficient nutrition of the individual would leave its impress upon growing feathers, it is not likely that it would, in the case of a moulting bird, affect one phase or stage of feather growth without affecting all stages.

Each feather has its own cycle of growth, and the supply and quality of the nutrition for the perfection of its different parts must vary with each stage of growth, independently of degree of blood-pressure dependent upon food-supply. Hence we should not like to say that "The formation of the quill is probably the direct result of a progressive diminution of an already lessened food-supply," but that it was due to the normally modified supply and character of the nutriment furnished by the blood-vessels to the feather at this particular and final stage of its

[3] Jones, Lynds. The Development of Nestling Feathers. Lab. Bull. No. 13, Oberlin College. Noticed in *The Auk*, January, 1907, p. 90.

growth; or that the answer to Mr. Riddles's question, "What causes the production of 'down'?" is to be found in malnutrition of the individual.

J. A. A.

VERTEBRATE PALEONTOLOGY

New Fossil Mammals from Egypt.—It was announced some time ago that the expedition of the American Museum of Natural History to the famous fossil beds of the Fayûm had been highly successful, and particulars of the results have been awaited with much interest. Professor Osborn has just issued a short paper[1] describing some of the more remarkable discoveries. Two new forms, unfortunately represented only by portions of the lower jaw, are so peculiar that their ordinal position remains uncertain. One of these is named *Ptolemaia lyonsi,* and is taken as the type of a new family Ptolemaiidæ. It is even stated that it possibly represents a new order. The other, *Apidium phiomensis,* new genus and species, "was evidently a small omnivorous or frugivorous form with partly cuspidate teeth"; but at present its precise affinities are unknown. Two other fossils are described, representing new genera (Phiomys and Metaphiomys) of rodents, placed in the family Eomyidæ.

T. D. A. C.

Errata: The title of the article by Professor George H. Parker in the September issue, p. 601, should read "The Origin of the Lateral Eyes of Vertebrates." The figure on p. 606 is inverted.

[1] *Bull. Am. Mus. N. Hist.,* XXIV, 265–272, March 25, 1908.

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FURTHER STUDIES ON THE ACTIVITIES OF ARANEADS[1]

PROFESSOR THOS. H. MONTGOMERY, JR.
UNIVERSITY OF PENNSYLVANIA

1. AGE DIFFERENCES IN THE SNARES OF TWO ARGIOPIDS

To the best of my knowledge there has been made no comparison of the snares of immature and adult spiders, with regard to the problem of whether such snares become more complex as the animal grows older. Yet this is an interesting question in its bearings upon the perfection of an activity through repeated effort.

During the past months of July and August I have studied this matter on two common species of argiopids, *Epeira sclopetaria* (Clerck) and *E. marmorea* (Clerck), both of which construct large vertical, orbicular snares that are very favorable for measurements and the architecture of which has been well described by McCook.[2]

My observations were made at Woods Hole, Mass., where there was a large colony of *sclopetaria* in the laboratory buildings and beneath the boat wharves, and another of *marmorea* in a marshy woodland. All the webs measured were those in the free and natural conditions, except those of the newly hatched; to obtain the latter I kept cocoons until they hatched, then freed the young upon the window panes of my room where they spun their first snares. *Sclopetaria* makes cocoons throughout

[1] Contributions from the Zoological Laboratory of the University of Pennsylvania.

[2] American Spiders and their Spinning Work, Philadelphia, 1889–93.

the summer, and one female under observation furnished four successive ones (all made in the night); they hatch on the twenty-fifth or twenty-sixth day. *Marmorea* does not construct cocoons until the fall. Comparisons were made on the following points: (1) number of radii, (2) number of spiral loops, (3) greatest diameter of the spiral (orb proper). The spiral loops examined are those of the outer viscid spiral which is the true trap of the web, and the number of its turns were counted in that segment of the orb where they were most numerous (generally in the region below the central hub). A slight error is sometimes encountered in counting these loops for occasionally the innermost of them are scarcely distinguishable from the inner non-viscid spiral, but this is an error of only small amount.

The following table gives in condensed form the measurements of 265 snares. On the left is entered the species, sex and age, the linear measurements are in centimeters, the remainder is self-explanatory.

	Radii			Spiral Loops			Snare Diameter		
	Number of Counts	Extreme Numbers	Average Number	Number of Counts	Extreme Numbers	Average Number	Number of Counts	Extreme Sizes	Average Size
E. marmorea:									
♀♀, adult	87	19–43	28.3	87	29–71	48.2	86	18.5–48.3	28
♀♀, penultimate instar	19	21–35	27.8	19	16–61	48	19	16.5–35.6	23.4
♂♂, penultimate instar	16	23–36	28.3	16	26–61	41.3	16	14 –30	20.6
♂♂, antepenultimate instar	3	19–34	27.3	3	37–39	38	3	19.6–25.4	22.1
Young from .3–.6 cm.	23	19–35	28.7	23	16–51	29.5	21	7.6–28	15
E. sclopetaria:									
♀♀, adult	24	15–24	19	21	26–56	35.4	24	24.1–48.3	35.6
♂♂, penultimate instar	2	18–23	20.5	2	:4–30	27	2	20.3–30.5	25.4
Newly hatched	91	11–20	15.3	91	11–23	16.2	91	5.1–11.9	7.6

With regard to increase of complexity of the snare with advance of age of the spider this table shows us the following figures for *sclopetaria*. The first formed snares, those of the newly hatched, exhibit an average of 15.3 radii, 16.2 spiral turns and 7.6 cm. diameter in comparison with averages of 19. radii, 35.4 spiral turns

and 35.6 cm. diameter of adult females. In other words while the diameter of the orb increases nearly five times, the number of spirals becomes slightly more than doubled, and the number of radii are increased less than one quarter. For *E. marmorea* the webs of immature individuals of from .3 to .6 cm. were compared with those of adult females, and the table shows that between these ages the number of radii remains about constant, while the number of spiral turns and the diameter of the spiral about double themselves; females in the penultimate instar show the orb almost as complex as that of females in the last instar.[3] For both of the species examined, accordingly, the age changes in the snare are greatest with regard to the diameter of the viscid spiral, less with regard to the number of its loops (on the average these only doubling their number), and least with regard to the number of the radii.

It is interesting that the first snare of the spiderling has all the parts of that of the adult, namely, the central woven hub and the inner non-viscid spiral in addition to the viscid spiral, radii and foundation lines. With increasing age of the spider the threads of the snare become thicker, the whole structure larger, but otherwise beyond the addition of a few more radii and a doubling of the number of the spiral turns there is no particular change effected. The newly-hatched show also about the same specific habits as do the adult: in *marmorea* the young, as does the mother, remains in a nest in a curled leaf holding communication with the snare only by a trap-line; and in *sclopetaria* the young, again like the mother, remains either at the center of the snare or else away from it, holding a trap-line but not hiding within a nest. Further, though there are frequently imperfections in the snares of the young, such as incomplete radii, asymmetri-

[3] By last or ultimate instar is meant the one of sexual maturity, even though this may be, and in some species regularly is, followed by other moults; the penultimate instar would be the next preceding, and the antepenultimate the one before that.

cally placed spirals and imperfect meshing of the hub, such imperfections seem to be quite as usual in adult webs so that it is rare in either of these species to find perfectly symmetrical webs. The adult spider can not be said to construct a more serviceable snare than does the spiderling, for the spiderling's is really much larger in diameter in proportion to the size of the body. And while the adult has about twice as many spiral loops, the spiderling with his fewer loops probably secures all necessary nourishment to the same extent as does his mother. Thus with the growth of the spider the snare does not become more serviceable as a trap. In all this excellent architecture the young as well as the adult labors first to make a scaffolding to support its weight, then lays down upon this the food-gathering spiral; and it does this quite as efficiently as does the adult. We might conclude that the number of spiral loops becomes larger because the supply of available silk has greatly increased; and that more radii are added because the weight of the spider increases faster than the size of the web, and because the spider in all her building tests the strength of the scaffolding, adding a new line wherever the structure sags. But the increase in number of parts can not be ascribed to intelligence, or memory of reiterated experience, for the mother seems to continue the same instinct possessed by the young and shows no peculiarity in the spinning process not exhibited by the latter. The age differences of the web are, accordingly, due mainly to: (1) increase in the weight of the spider in combination with the instinct to make the scaffolding sufficiently strong; and increase of size of the spinning organs, therefore of silk substance. The spider does not exhibit learning at any stage, for it constructs the first web with as much ease and certainty as any later one. In this connection I may also mention, as the result of many observations, that the spider makes the first cocoon as perfectly as any subsequent cocoon; and when it makes a mistake at any part of the process of cocoon spinning seems unable to rectify it.

The absolute size of the snare and the number of spiral loops vary much in individuals of the same species. The size is dependent upon two factors: (1) size of the space in which the web is spun, and (2) amount of silk available. If confined in a cramped place the spider spins no snare at all, as I found by attempting to induce them to spin in cages made of two panes of window glass separated by a wooden rim 3 cm. thick. Then if successive webs are destroyed soon after making each contains fewer parts than its predecessor, which can be ascribed only to deficiency of silk. Thus with one adult female of *sclopetaria* her first snare had 21 radii, 35 spiral loops, and a diameter of 37 cm.; this I destroyed, and her second made a day or two later had 17 radii, 25 spiral loops and a diameter of 30.5 cm.; a week later I destroyed this and she made a third with 18 radii, 25 spiral loops and diameter of 24.1 cm., then (after demolition of this one) a fourth with 19 radii, 19 spirals and diameter of 23 cm.

In orbs of adult females, particularly of *marmorea,* the space between neighboring spiral loops varies greatly in size, whence it follows that the diameter of the orb is no index of the number of spiral turnings, and that different females must use different parts of the body as a measure of this space. This is really the most marked variation to be found in orbs, and it is shown just as well in those of spiderings.

2. The Snares of Male Argiopids and the Number of Males

In this conjunction I wished to compare the spinning activities of males of *Epeira marmorea* and *E. sclopetaria* with those of their females. On this matter McCook has to say:[4]

> As a rule, the spinning abilities of male spiders, as far as they relate to the capture of prey, have been shown in Volume I to be less decided than with females. The rule is not absolute for all species, as in some cases the snare spun by the male is precisely like that woven by

[4] *L. c., 2,* p. 65.

the female. But in certain other genera, as, for example, Argiope and probably Nephila, the snares of the male are rudimentary, and do not compare in perfection with those of the female.

The immature males of the two species studied by me construct perfect snares of the types of those of their respective females. But the adult males of *marmorea* (no adult males of *sclopetaria* were examined) do not spin snares at all but build nests near those of adult females and live on the outskirts of the snares of the latter; this was the case with all of the 23 mature males found in the latter half of the month of August.

Data on the snares of immature males are condensed in the table already presented. The snares of orbs of 16 males of *marmorea* in the penultimate instar show the same average number of radii, a somewhat smaller average number of spiral loops (41.3 to 48), and a smaller average diameter (20.6 cm. in comparison with 23.4 cm. and 28. cm., as compared with snares of females of this species in the penultimate instar and at maturity. Data for the snares of 3 males in the antepenultimate instar show somewhat lower averages. Those of 2 males of *sclopetaria* in the penultimate instar, show, on comparison with adult females of this species, a slightly greater average number of radii (20.5 to 19), a smaller average of spiral turns (27 to 35.4), and a smaller average diameter (25.4 cm. to 35.6 cm.). That is to say, males in their penultimate instar construct fully as many radii as do females in their penultimate or even ultimate instar, but a smaller number of spiral turns and they make smaller snares. But a male in his penultimate instar is considerably smaller than a female of the same age, therefore in proportion to his size and weight his snare is quite as complicated as that of the female and is in no sense rudimentary. It would appear, accordingly, that the spinning instinct, so far as the snare is concerned, is as perfect in the male as in the female. He makes no web when mature because the sexual impulse completely overcomes the desire for food, hence the instinct for snaring it, though

he does continue to construct nests; and his nest is quite as complex as that of the female. I have not determined whether a male after satisfaction of his sexual desires would again spin a snare; but probably he would not have a chance of doing so, for the female becomes satisfied before he does and frequently succeeds in devouring him. Indeed, I have obsrved a female of *marmorea* devouring one male while another was importunely making advances to her.

As to the sexual ratio of *mormorea,* I found in the field 16 males of the penultimate instar to 19 females of the same age, and 23 adult males to 87 adult females. These figures are too meager to allow of any general conclusion, beyond that the males at maturity seem to be less than half as numerous as females, and just before maturity to be slightly less numerous. The greater disparity in numbers at maturity may well be due to accidents befalling males while they are seeking mates and to their destruction by the females themselves. On August 31 I measured the orbs of 24 adult females of *marmorea;* on only 8 of them were there adult males, these webs having from one to three males each. It is probable that more than one male copulates with a given female, and that a given male may mate with more than one female; for I have found this to be the case with *Theridium tepidariorm* and certain Lycosids.[5]

3. The Senses of Touch and Sight in Snare-making Spiders

The number of eyes in araneads, usually eight, their different positions upon the head area, and their complexity in being compound (constructed of separate retinulae), has led naturalists to the view that the sense of sight plays a large part in their vital activities. And this idea is substantiated for such species as are strictly hunt-

[5] Before the antepenultimate instar males can not be distinguished externally from females. According to W. Wagner (La Mue des Araignées, *Ann. Sci. Nat.*, 1888) the external male peculiarities do not exhibit themselves in *Attus* before the fifth moult, and in *Lycosa* before the seventh.

ers and not snarers, and particularly for the diurnal Attidae as demonstrated by the studies of the Peckhams.[6] But among the snare-weavers I feel positive, in agreement with McCook's conclusions, that the sense of touch almost completely supplants that of sight. Long observation in the field and especially upon species kept under control has led me to this opinion, the main reasons for which may be briefly mentioned. The lines of the snare are the medium by which the spider secures its food and conducts its mating, all by touch. In the operation of spinning, whether it be a snare or a nest or a cocoon, the process is conducted beneath the ventral surface of the spider, accordingly, in a position removed from its field of vision; and all such architecture is frequently carried on in the dark of night. With the true orb-weavers, the argiopids, the spider sometimes remains at the center of the orb holding tensely with its tarsal claws various radii and thereby feeling any object that strikes the web. In this position she can see only a small part of the snare, if any of it, yet she instantly perceives any impact upon any part of the snare. Or the spider does not rest upon the snare at all, or comes out upon it only at night and twilight, remaining in a nest at some distance from the snare; in that case the spider perceives any shock to the snare by means of the trap-line that passes from her claws to the center of the snare, such a trap-line being a modified radius. McCook (*l. c.*) has given an admirable treatment of the use of this trap-line and of how it is often employed to spring the snare. Thus *Epeira marmorea* remains through the hours of sunshine for the most part in a nest within a leaf that has curled up, where she can not see the web at all, and feels every motion of it through the connecting trap-line. And it is instructive to watch her when an insect agitates the snare. She then rapidly pulls the trap-line several times, thereby learning that the prey is struggling in the web, runs

[6] Peckham, G. W. and E. G. Sense of Sight in Spiders. *Trans. Wisconsin Acad. Sci.*, 1894.

rapidly to the center of the snare, then locates the insect precisely by pulling successively different radii. In this food-gathering she seems to use touch alone, and it is questionable whether she at any time sees her food, for even in the process of mastication and sucking she holds it beneath her head. And this sense of touch is so delicate that by it the spider can to some extent determine the nature of the object that causes the impact, as, *e. g.*, whether it be large or small.

Likewise with the mating, that I observed this summer in *Epeira marmorea.* The female was near the center of her snare hanging vertically downward with her dorsal surface, her vision area, away from the male. He was at the outer end of one of her radii and though his head was turned towards her he perceived her position and tested her inclinations not by sight but by touch communicated through that radius; they signalled to each other by pulls and counter pulls of the line, he climbed along the radius towards her, at nearly every step repeating his pulling, then when about an inch away he advanced rapidly to press his palpi against her epigynum while she drew in her extremities close to her body. Each such act was only of momentary duration, and at its end he moved away along the same radius, repeated his signalling, then again advanced towards her; thus there were numerous repeated copulations during the half hour I watched the pair.[7] The female never saw the male at all, and he perceived her so far as I could determine by the sense of touch alone. In an earlier study, where I

[7] Previous observers of European species of this genus have described this process in much the same way. Compare:

Walckenaer. Histoire naturelle des Insectes. Aptères. Suites à Buffon, 2, Paris, 1837.

Menge, A. Ueber die Lebensweise der Arachniden. *Schriften naturf. Ges. Danzig*, 4, 1843.

Menge. Preussische Spinnen, I. *Ibid.* (N. F.), 1, 1866.

Termeyer, R. M. de. Researches and Experiments upon Silk from Spiders, etc. Translated by Burt G. Wilder, *Proc. Essex Inst.*, 5, 1866.

Lendl, A. Ueber die Begattung der gekrönten Kreuzspinne (*Epeira diademata* Cl.). *Termész. Fuzetek, Budapest*, 10, 1886.

described this act in much greater detail for various other species,[8] I had called attention to this exclusive use of touch in the courtship and copulation of snare-weavers. The female responds to the male's signals by more gentle and weak pulls when she is eager for him, by stronger and more aggressive ones when she regards him as an object of food; thus there is a language of touch, even at a distance, and the male assures himself, if such an expression is permissible, of the nature of his partner's responses. In the case of *marmorea* just described the male took effective means to procure his escape should the female prove aggressive, just as did the male of *E. diademata* observed by Menge: while advancing along her web radius he held an escape line of his own, the outer end of which was attached to the periphery of her web; and when her motions were more violent than usual he loosed his hold on her radius to drop and swing out of her reach on his own escape line. In this way he procured the double advantage of escape and of remaining in communication with her web.

It may be noted in passing that while in *E. marmorea* the male seeks only adult females, in *Theridium tepidariorum* the males mature somewhat earlier than the females and are to be found upon the webs of the females before the latter have matured.

We can say that among araneads the sense of touch is the dominant one in those that are snarers. Spiders lack hearing, as seems to be proved by the experiments of my student Miss Pritchett.[9] The long spines placed upon the limbs seem to be tactile and not auditory organs. Spiders possess the olfactory sense but it is not known how much they are guided by it. The primary sense of the snarers is touch, and they possess it to a

[8] Studies on the Habits of Spiders, particularly those of the Mating Period, *Proc. Acad. Nat. Sci. Philadelphia*, 1903.

[9] Pritchett, A. H. Observations on Hearing and Smell in Spiders. Amer. Nat., 38, 1904. These observations have been criticized by F. Dahl (*Naturwiss. Wochenschr.*, N. F., 4, 1905), but Dahl never instituted crucial experiments such as those of Miss Pritchett.

degree of perfection hardly equalled by any other terrestrial animals.

The question then presses, of what use are the eyes to snare-weavers when their sensations are so particularly tactile? The newly hatched spiderlings evidently use their eyes for they are always positively phototropic while the adults are generally negatively so. This turning towards the light benefits the spiderlings and consequently the species by serving to disseminate them from the home area into new feeding grounds. And I believe it is a quite general phenomenon among all animals whose adults are more or less sedentary and tubicolous, negatively phototropic, for the young to be at first positively phototropic, though I do not know whether any one has drawn attention to the comprehensiveness of this principle; in this most wide-spread kind of migration the beneficial result of the change of tropism is to prevent overcrowding. But as the young snare-weaver grows older and begins to avoid the light as does its parent, it does not employ its eyes in the primal acts of feeding and mating but mainly determines by them the source of the light in order to avoid it. Despite their complexity, accordingly, the eyes of snare-weavers, when they have passed infancy, seem to be used mostly as direction eyes. This being the case it seems strange that these eyes should have retained the complexity inherited from hunting forefathers, and it is possible that they have come to subserve some other new function, as, *e. g.*, to have become thermic receptors; this might well be determined experimentally. At any rate we shall have to change current views as to the rôle of vision in spiders.

4. On the Average Duration of Life in Araneads

In the case of all species that I have studied adult males are found during only a short period of the year, for perhaps not longer than a month or six weeks, and in latitudes where there is a marked winter season they do not live over this period of cold. And from observations on *Theridium tepidariorum* I estimate from the rate

of growth that this species is able to reach full size in one year. Males, accordingly, live for only a relatively short time as adults, and their life time would seem to not exceed one year. In my observations on *Epeira marmorea* I found on July 25 among 16 recognizable females (in young of 8 mm. body length or less the sexes are externally indistinguishable) only 5 adults, while on August 31 out of 24 females all but 3 were adult; these data indicate for this species that while at the beginning of the summer few females are adults, at its end most are. It is then probable for this species, though not proved, that few females live over from one breeding season to another, and then only under favoring environmental conditions, a conclusion reached by McCook for *Argiope.* But the females live at least some months longer than the males for they are to be found later than the breeding season and after all males have disappeared; and there are cases on record (cf. McCook) where females of certain species have been kept from two to seven years. I have described for *Latrodectus*[10] how the mating occurs in the late winter at Austin, Texas, the adult males are not found after this season, while the females continue to produce cocoons until the following autumn. We might say in general that males of spiders probably do not live longer than one year, females some months longer or in certain cases several years.

5. The Cocooning of Loxosceles rufescens Duf

I give these brief notes here because the cocooning of no sicariid has been hitherto described, and because it may be of some interest from the standpoint of comparative architecture. The cocoon of *Loxosceles* is sessile, attached to the snare, so resembling that of *Sicarius,* while in *Scytodes,* the only other genus of the Sicariidae for which the cocoon has been described, it is carried in the chelicera of the mother.[11]

[10] *Jour. Exper. Zool.,* 5, 1908.

[11] I have taken these genera as defined by E. Simon: Histoire naturelle des Araignées, 2me éd., Paris, 1892.

This is an abundant form at Austin, Texas, where it makes a large and irregular web beneath logs and stones, usually in drier situations. In its movements it is the most languid and timid species I have ever seen, waiting quietly until its prey has inextricably entangled itself in the web, and feigning death for a remarkably long period. Both males and females are able to undergo thirst for weeks at a time, an unusual faculty among spiders, and to this ability it probably owes its success under the desiccating Texan sun.

On June 13, 1907, I placed six females in separate glass cages. Four of them when first found had each a single cocoon, and each produced cocoons in captivity to the number of from two to four each. One of them produced five cocoons in all.[12] The season of cocooning evidently extends through the whole three months of the summer.

The cocoons are discoidal, with diameter longer than the spider's body, and are made in the mornings from seven o'clock to noon. In the two cases where the operation was observed they were spun against a vertical wall of the cage, not placed horizontally. After making the base, a process not seen, the spider remains quietly above it until the following day, a cessation of activity quite unique among araneads but thoroughly in accord with *Loxosceles's* quiet disposition. Then the eggs are laid upon this base, an act that occupied eight minutes in the case where it was followed. Over the egg mass the mother spins a thin-textured cover, swaying the spinnerets leisurely back and forth; this cover spinning occupied one hour in the case where it was timed. The mother remains upon the cocoon until it hatches.

[12] Some naturalists write as though multiple cocoons were a rather exceptional phenomenon among spiders. On the contrary I believe it is the general if not universal rule, for I have found it to be the case also in lycosids, pisaurids, attids, agalenids, thomisids, clubionids, drassids, theridiids, argiopids, dictyniids and filistatids.

NOTES ON THE DAILY LIFE AND FOOD OF CAMBARUS BARTONIUS BARTONI[1]

FLOYD E. CHIDESTER

In all animals we find that there are periods of activity and rest. During the active period, we find such interesting phenomena as feeding, copulation, and, in some animals, a very interesting series of movements connected with the care of the young.

My study of the daily life of the crawfish is one of a series of studies instigated by Professor C. F. Hodge in the effort to arrive at some accurate data as to the work performed by various species.

Crawfish were kept in two different aquaria during the winter of 1907-'08, and their actions watched closely.

One tank was an ordinary running water tank with a pile of sand at one end, and containing, in addition to crawfish, at times, trout eggs, young trout, frogs, clams and a turtle. There were also, all the time the crawfish were kept there, several tufts of the common water weed, Fontinalis, floating in the water.

The other tank was a heavy glass aquarium, measuring on the inside, 1 x 1½ x 2 feet 8 in. This aquarium was elevated about an inch at one end, and beginning at the other end, a mud and sand bottom sloped gradually upward to a level bank which was covered with moss and grass and kept moist

In the aquarium was a clam to assist in clearing the water, a water hyacinth, and some more of the water weed mentioned above.

At different times, as I experimented with the food of the crawfish, there were bits of fresh meat, sprouts, eggs and young of trout, toads, frogs and salamanders; dead frogs and fish, and dead crawfish.

[1] Contributions from the Biological Laboratory, Clark University.

The water was changed daily and oftener at feeding time, during the entire winter, and record kept of the activities of the crawfish. It was not until spring, however, that night and day observations were made.

During the fall and winter, up to February 1, frequent cases of copulation were observed. Contrary to Dearborn's statement, '00, I found that the males do not know the females and that males repeatedly grasp other males, and sometimes, in spite of their frantic struggles, turn them over and attempt to copulate with them. The difference in behavior in the case of the male, when thus grasped, is that he continues to resist violently at intervals, until released, while the female, as soon as grasped firmly, ceases to struggle, and lies passive.

Another interesting thing was noted in connection with the actions of crawfish before moulting. In the case of adult crawfish with hard exo-skeletons, I found that for two or three days before the ecdysis, they would come up partly out of the water, so that the carapace was entirely out of the water, and dried out thoroughly.

Crawfish when transferred from the running water tank to the still water one, would almost immediately seek cover, generally burrowing into the bank, and remaining during the day with their heads toward the entrance, quiet unless disturbed.

In the still water aquarium, there were at one time, six crawfish hibernating in the bank, with their burrows stopped up, for three weeks. The other seven in this tank were in the deep water under plants during the day, but, as darkness fell, they came up into the shallows and on the bank.

Repeatedly, I have come into the building after darkness had set in, and seldom failed to find several crawfish on the bank.

Crawfish are generally supposed to be omnivorous. They are not, however, so fond of decayed matter as has been supposed. Tests made in the laboratory show that, when they refuse to eat stale food, they will eagerly con-

sume fresh. They will eat fish which have been recently killed, in preference to partly decayed ones.

In the spring, after moulting, there seems to be a consuming hunger. I have seen, at about 9 P. M., a crawfish within about six inches of the bank of a small pond, so intent on pulling to pieces and devouring a partly decayed fish, that he did not notice the very strong acetylene light that I held close to him.

Experiments with lights of various intensities, elucidated the fact that crawfish are negatively phototactic to strong light but positively phototactic to weak light.

Raw and cooked meat of all kinds, worms, dead fish, pieces of clam, moulting crawfish, and dead crawfish were eaten by the crawfish in confinement. They are said to eat their own cast-off coats, but although these were left in the aquarium for about a month, they were undisturbed.

Tests were made to determine if the crawfish would eat fish (trout), frog and toad eggs. Very few were eaten, and these few when the crawfish had had nothing to eat for ten days, and had nothing else to eat.

Young frog and toad tadpoles were kept in the aquaria and lived happily for a long time.. To determine if crawfish eat toad or frog tadpoles, twenty-five toad and frog tadpoles were placed in a shallow dish, and, with a renewal of water every day, kept for four days with a single, supposedly hungry, crawfish. Of the twenty-five tadpoles, in all, but eight were eaten.

About two weeks later, when the tadpoles had become quite a little larger, a test was made with toad tadpoles. A male crawfish was placed in a shallow aquarium jar with twelve live tadpoles, and kept for three days, with change of water twice a day. It was not until about fifty hours had elapsed that he ate of the tadpoles, and then he ate but one.

A female crawfish was put into an aquarium jar at the same time as the male, with 12 live toad tadpoles. This was at 5 P. M. At 6 P. M., she had eaten all but one of them. At 6 P. M., 17 more were put in, making 18 in all.

At 10:30 P. M., five more tadpoles were gone. At 9 A. M., on Friday, only 5 were left, one of these being dead. This was a record of 22 out of 27 active tadpoles in 16 hours. The female was seen to catch several of the tadpoles, using for this, not her cumbersome chelæ, but her smaller, nimble, first pair of ambulatory appendages.

Evidently *Cambarus bartonius bartoni* is capable of catching toad tadpoles, but it is improbable that many are caught, for I am informed by Mr. Newton Miller that the young tadpoles, although near the shore during the day, go to the deeper water at night. It is at night that the crawfish come into the shallower water near the shore, and even part way out of the water. Here it is that they may catch an occasional fish, frog or toad.

Two young frogs were kept during the greater part of the winter in one of the aquaria on my desk with the crawfish, but none of the dozen seemed able to kill them. Once I forced a frog to swim down to one corner of the tank where several crawfish were collected, and one of the crawfish grasped a hind leg with his right chela, and a moment later secured the front leg on the same side with his left chela. He then forced the frog to the bottom and attempted to pull him limb from limb, all the time holding the animal under water. In just a moment, however, the frog kicked with his free hind leg, and accidentally striking the crawfish on the carapace, was released.

My observations and experiments in the laboratory were supplemented by many evenings spent on the shores of several small ponds near the university, observations being made by means of a strong acetylene light. I believe, in the light of these observations, that the crawfish in the still water aquarium behaved normally.

In the spring, the crawfish is very active, and feeds with much more eagerness than during the winter. It is then, too, that the interesting phase of the mother's care of the eggs may be best seen.

On account of this, I took occasion to watch a pair of crawfish, a male, and a female with eggs just about ready

to hatch, through 24 consecutive hours, beside several observations of lesser duration.

In these observations, I was aided by Dr. C. F. Hodge and Mr. Newton Miller, who kindly gave me occasional resting periods.

The first set of observations which I shall record were made on May 16–17, 1908.

Observation was begun at 6 P. M. on two crawfish, a male and a female with eggs about ready to hatch, and lasted until 6 A. M. the following day. In the aquarium with the crawfish, were the water hyacinth and Fontinalis mentioned above, some young sprouts, five young toad tadpoles, and some pieces of fresh meat.

The male was moderately active between 8.10 and 8.45 P. M., most active between 12. and 1.30 A. M., and had a lesser period of activity between 2.05 and 2.30 A. M. The longest period of quietude was from 1.30 to 2.10 A. M. He ascended and descended the bank nine times during the 12 hours. The male did not feed.

The female ascended and descended the bank 84 times during the 12 hours. She ascended and descended 17 times between 1 and 2 A. M. She would climb the bank and aerate her eggs in the open for several moments, then retire to the deep water and almost immediately return to the bank. The greatest activity was from 11 P. M. to 6 A. M. She fed at 6.50 and again at 7.07 P. M. both times on the fresh meat. Her longest rest period was from 10.30 to to 11 P. M.

The next series of observations was performed on three crawfish, the two observed on May 16–17, and in addition, a female without eggs. This time observation was kept up for 24 consecutive hours, from 1 P. M. May 19, to 1 P. M. May 20.

The same kind of food was used as before, care being taken to avoid fouling the water with it until about one-half hour before the records were taken.

The male fed a great deal this time on the fresh meat, feeding from 1.35–2.15 P. M., 2.30–245 P. M., 3.18–3.40 P.

M., 3.48–5.00 P. M., 4.10–4.30 P. M.

He was most active from 11.35. P. M. to 3.15. A. M. It is interesting to note that each period of feeding, if lengthy, was followed by a correspondingly long period of rest. The longest rest period was from 4.45 to 8.05 A. M. The male did not ascend the bank at all during the 24 hours.

The female with eggs began ascending the bank and aerating her eggs at 4 A. M. and stopped at about 4.25 A. M., then began again at 6.15 A. M. gradually lengthening the stay on the bank until 9 A. M. then shortening the frequency of the visits, and lengthening the stay in the water; this period of less frequent visits lasted until 11 A. M., then from 11 A. M. to 12 M., there was great regularity of aeration, and from 12 M. to 1 P. M., less frequent aeration. Ascent of the bank was made thirty-four times during the 24 hours.

Feeding was done at 1:45 P. M., and again at 2.15 P. M., but in neither case did it last longer than ten minutes.

Number seven, a female without eggs, was very inactive, staying under a stone the greater part of the time. She came out on the bank but three times. Her period of greatest activity was between 3.30 and 4.15 P. M.

From these observations of the crawfish in nature and in the laboratory, we may conclude as follows:

1. Crawfish are most active at night.

2. There is marked activity at nightfall and at daybreak.

3. Feeding is generally done at night, but may occur during the day.

4. In the spring, the crawfish eats much more often than during the winter.

5. *Cambarus bartonius bartoni* prefers fresh animal food to anything else.

6. Feeding is followed by rest, prolonged periods of feeding being followed by equally prolonged periods of rest, the animal not becoming active for several hours.

7. There is apparently no spontaneous play or exercise, movements being purely utilitarian.

8. A female aerates her eggs both on land and in water.

9. Crawfish come up into the shallows and elevate their carapaces partly out of the water.

10. Combing or cleaning movements are executed by means of the first and second ambulatory appendages. These consist in scraping the carapace.

11. Males do not distinguish between the other males and the females, and frequently grasp males and attempt to copulate with them.

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SOME POINTS IN THE ECOLOGY OF RECENT CRINOIDS

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Although a considerable amount of work has been done on the anatomy of various species of recent crinoids, the embryology and development of two species, closely allied, are well understood, and the systematic side of the question has received more or less attention, little has been accomplished in the elucidation of the interrelation of the crinoids and the other classes of marine invertebrates, or the relation of the crinoids to marine conditions in general. This is undoubtedly due to the rarity of the group, and its chiefly inaccessible habitat, rendering it, as a whole, a difficult subject for extensive research; but much may be learned from the data already recorded, and it is the purpose of the present paper to suggest certain lines along which much of interest may be done on the basis of the present numerous, though scattered, records.

It has long been known in regard to *Antedon bifida* of the coasts of Europe that specimens taken in deep water are larger than those taken in shallow water or along the shore, though no plausible reason has been shown for the phenomenon. It has been suggested that the coldness of the deeper water may stimulate it to greater development; but specimens from different localities, taken at a considerable difference in depth, yet with the same bottom temperature, will vary greatly, those from the greater depth being much the larger; similarly, specimens from the same depth, but with marked difference in the bottom temperature, will be found to be of practically the same size. As, however, specimens from very shallow water are usually about 120 mm. in expanse, while those from deep water are 220 mm. or more, it is evident that some important factor is involved.

The food of crinoids consists of very small pelagic organisms and minute crustacea. At or near the surface the crinoid must depend upon those which swim within reach of its pinnules or which it may intercept by the slow movement of its arms; but in deeper water while this source of supply is just as available as at the surface, the crinoid gets, in addition, all the carcasses of those organisms in the levels above it which die and are precipitated to the bottom. The intensity of this rain of food increases proportionately with the depth, so that the deeper a crinoid lives, the greater is the available food supply; consequently, the better nourished will be the individual and the greater its size.

We see, therefore, that the size of *Antedon bifida* appears to be merely a question of food supply. Passing from a single species to a consideration of the group in general, we find that the average size gradually increases from the shore line to about the 100 fathom mark; this is plainly due to the gradual increase in the supply of food, as just explained; from 100 fathoms to about 600 fathoms the same size is maintained; but below 100 fathoms plant life, and with it the host of small organisms dependent directly or indirectly upon it, upon which (as well as upon certain of the minute plants) crinoids are dependent for food, begins to disappear. This gradual disappearance of vegetable organisms and their dependents is offset by the gradual increase in the rain of carcasses from above, so that an equilibrium is maintained down to about 600 fathoms, and hence the size of the crinoids remains about the same from the 100 to the 600 fathom mark. Below 600 fathoms, the gradual decomposition of the rain of carcasses progressively lessens its food value, and, therefore, we note a decrease in the size of the crinoids, hardly noticeable at first, but soon becoming more marked, until, below 2,000 fathoms, we find only the minute comatulid Bathymetra and the equally minute stalked Bathycrinus.

By this hypothesis the general absence of the Pen-

tacrinitidæ above 100 fathoms is at once explained; the stalked pentacrinites (Encrinus, Endoxocrinus and Hypalocrinus) are animals of very considerable size; besides a large crown they have a bulky stem which must be nourished, and the organisms found at or near the surface are not sufficient to support them; it is not until the depth of approximately 100 fathoms is reached that the organisms occurring in the water about them, plus the cumulative effect of the rain of dead from a belt 100 fathoms in depth, acquires sufficient intensity to admit of their existence. Incidentally, their remarkable uniformity in size is explained; for the recent pentacrinites inhabit almost exclusively the 100–600 fathom belt, which has just been shown to be a belt of uniform crinoid size. A species of Endoxocrinus, *E. wyville-thomsoni,* and the peculiar Hypalocrinus both descend to over 1,000 fathoms, but both are much smaller than their relatives above the 600 fathom line.

The common arctic comatulid, *Heliometra glacialis* (= *eschrichtii*) occurs from east of the Kara Sea to westward of Greenland, thence southward to off Nova Scotia;[1] the southern part of the Sea of Okhotsk and the northern part of the Sea of Japan are inhabited by a variety, *maxima*, differing only in its great size. This species varies greatly throughout its wide range; north of Europe it is small, though rather larger around Spitzbergen; off Halifax and on the Grand Banks it reaches a comparatively large size, while off the western coast of Greenland it attains a diameter of 500 mm. or more, reaching 700 mm. in the Okhotsk and Japan Seas.

The west coast of Greenland abounds in fjords which are continually giving off fresh water ice which floats away, melting as it goes, thereby killing millions of small organisms which are unable to endure a great change in the salinity of the medium they inhabit; these fall to the bottom and furnish an abundant supply of food for the

[1] Stimpson's *Alecto eschrichtii* from Grand Manan is in reality *Hathrometra tenella.*

crinoids there, which consequently are enabled to attain very considerable dimensions. In the Kara and Barents Seas there is no such supply of fresh water at hand, hence the crinoids are small, but Spitzbergen, through its snow fields, and the consequent freshening of the surface water about it, allows the crinoids along its shores to reach a larger size than those of the Barents and Kara Seas, though they are not nearly so large as are those from west Greenland.

Over the Grand Banks the Gulf Stream brushes by, and mixes more or less with, the cold northern current; this is fatal to the delicate southern life it contains, which is killed and precipitated to the crinoids below; they, therefore, in spite of their living on the extreme southern limit of the specific range, are as large as, or larger than, specimens from Spitzbergen.

The Kuro Shiwo, or Japanese current, sends off a branch through the Korean Straits which washes the eastern shore of the Japan Sea, and in its northern part, from the Straits of Tsugaru to the Straits of La Pérouse mingles with the very cold water from the Okhotsk Sea. The mixing is very gradual and extends over a considerable territory, and over all this area the crinoids are of gigantic size, bearing witness to their enormous food supply. Now this colony of *Heliometra glacialis* var. *maxima,* a purely arctic species, replaced on the Pacific side of Japan and the Kuril Islands by widely different forms, and finding no close relatives nearer than the Kara Sea, might be supposed in the course of the years which have elapsed since the Okhotsk Sea was part of the Arctic Ocean, to have become rather widely differentiated from the parent stock, and to have gradually reached a larger adult size from some other cause than the question of food supply; fortunately, however, we are able to make some observations bearing directly upon this point. In this area, Heliometra is found where the bottom temperature is very low, about freezing or less; but dovetailed into these cold areas are others where the

bottom temperature is 40° F. or above. These warmer areas are occupied by a fauna radically distinct from the arctic fauna of the cold areas, though the depth is about the same, and we find in them crinoids belonging to the purely Pacific genera Thaumatometra and Psathyrometra. It is gratifying to note that the representatives of both these genera are far larger here than anywhere else, the difference, in fact, being relatively greater than in the case of Heliometra. These three genera here live among entirely different surroundings, and in widely different temperatures; but their food supply, coming in a rain from above, is the same, and is, moreover, the only common ecological factor; therefore, there is no room for doubt that the food supply is the cause of the great increase in size.

While the recent pentacrinites as a rule live below 100 fathoms, in certain places, such as in some localities along the northern coasts of Cuba and Guadeloupe, and in Suruga Gulf and Sagami Bay, Japan, they approach much nearer the surface, and have even been taken in water of between 20 and 30 fathoms (Guadeloupe). Now Cuba and Guadeloupe are mountainous islands, while Suruga Gulf and Sagami Bay are close to that magnificent mountain Fuji-Yama, and to other high lands as well. The result is that many intermittent streams flow into the sea at these places, having their origin in the high lands; the rise in volume of their waters is so sudden that the pelagic life can not give way before it, but is killed and precipitated. The greatly increased food supply in the vicinity of one of these streams thus brings the food intensity up to such a level that the large pentacrinites may exist in such localities in much shallower water than would otherwise be possible. The water from these streams is never very great in amount, and does not penetrate deeply, but spreads out over the surface of the sea; thus a crinoid could exist very near the surface without being affected by it. Large rivers with a comparatively steady flow, on the other hand, freshen the

entire sea for a large distance from their mouths, and thus render crinoid life impossible.

Within the tropics, particularly in the East Indies, very large comatulids belonging to the Tropiometridæ, the Zygometridæ, the Himerometridæ, and the Comasteridæ occur abundantly in very shallow water, often just below the low tide mark; moreover, they decrease in size with depth. This would appear to directly contradict the conclusion reached in the case of *Antedon bifida,* but in reality the problem is an entirely different one. Within the tropics the intense scorching sunlight causes rapid evaporation from the surface of the sea, especially where the water is shallow, and a consequent mortality among the more delicate organisms. The beaches and rocky shores, at low tide, warm up, to be covered again at high tide with comparatively cool water, full of organisms unable to stand a great difference in temperature, which are consequently killed and swept back into the sea, to fall just beyond the low tide mark. Periods of glaring sunshine are relieved by torrential rains, which are just as fatal to pelagic life through the sudden lowering in the density of the surface water. Thus it is evident that within the tropics the sublittoral zone and the sea bottom near the shore line offer the maximum food supply for the crinoids, and explain the occurrence in such localities of members of these four families of very large size.

But torrential rains are associated with mountainous districts; a glance at the distribution of the species of these four families shows that all of the large species and practically all of the small ones occur exclusively about mountainous islands or near high mainland, and they are particularly abundant along the shores of the larger East Indian Islands. On isolated coral reefs and about the shores of low coral islands where, owing to the very low altitude of what little land there is the rainfall is very small, these large littoral crinoids are quite absent.

The comatulids are divided into two great groups, one with triangular pinnules and small eggs, the Thalas-

sometroida, the other with round pinnules and large eggs, the Antedonoida. The forms with small eggs, being no smaller than those with large eggs, may reasonably be supposed to require a longer period for development. This would imply a greater duration of the free swimming larval period, which would result in greater powers of dispersal, hence a greater geographic range. Moreover, a slowly developing larva might be supposed to possess a greater power of adaptation to environment, and therefore a certain ability to colonize new places under changed conditions, for instance, to spread downward to great depths.

The genus Thalassometra, genus of the Thalassometroida (with small eggs) has the widest distribution of any comatulid genus known, geographically and bathymetrically. It is found throughout the tropics, northward to the Aleutian Islands, the West Indies and Portugal, and southward to South Africa, the Crozet Islands and Australia; in depth it ranges from about 50 to 1,600 fathoms. Charitometra and Tropiometra, two other genera of the same group, are both intertropical, and the former reaches very considerable depths. The genera belonging to the Antedonoida (with large eggs) are mainly comparatively local and do not occupy large bathymetric altitudes. Though a number are littoral and one inhabits the greatest depths from which crinoids are now known, the bathymetric range of each is small, far smaller than that of the genera of Thalassometroida.

The beautiful and brilliant coloration of the crinoids has often been remarked; so striking is the common European species, *Antedon bifida*, that it has formed the subject of colored plates by Heusinger, Dujardin, Dalyell, Dujardin and Hupé, and Gosse; but the larger tropical species are much more varied and handsome (though colored figures of them have been published only by Leach, and by Kuhl and van Hasselt) and are, for the diversity of their markings and the delicacy of their hues

unrivaled among the marine invertebrates. Observers have contented themselves with making short color notes, each on a very limited number of species, and no one has as yet made this phase of the subject an object of study, yet there appear to be many interesting points well worthy of record.

All colors are found in the crinoids except blue, though true black is confined to the disks of the Pentametrocrinidæ and to lines and spots on two species of Coccometra, and may therefore be omitted from a general discussion. Both blue and black, however, enter largely into combinations.

Yellow is the commonest color in the group, and is the color of all the more primitive forms, and of the young of almost all the others; it may, therefore, be taken as the fundamental basic crinoid color. The pentacrinoids of *Antedon bifida* are sometimes pink, though usually, like the pentacrinoids of the other forms in which they are known, yellow, and certain other forms are dull pinkish at all stages. We may, therefore, assume two basic colors, yellow and red, the latter an intensification of the former, found generally in the more specialized forms.

The derivatives from these two basic colors as they occur in the crinoids may be grouped as follows:

I. Yellow	+ [Blue] =	White. Green.
	+ [Black] =	Brown.
II. Red	+ [Blue] =	Purple; maroon. Violet.
	+ [Black] =	Crimson.

Under the first heading come:

Yellow: Bathycrinus, Rhizocrinus, Ptilocrinus, Phrynocrinus, Nanometra, Adelometra, Trichometra, Heliometra, Atelecrinus, and all but very large specimens of the species of Thalassometridæ.

White: Asterometra; markings on shallow water Thalassometridæ.

Green: Hathrometra, Coccometra, Leptometra, Compsometra.

Brown: Very large specimens of all the species of Thalassometridæ, Thaumatometra, and Thysanometra.

Under the second heading come, Zenometra, Psathyrometra, Bathymetra, Isometra, the Pentametrocrinidæ and Hypalocrinus.

No species is known which exhibits a perfect blending of these two basic types or their derivatives, though there are many mosaics in which both are found side by side, either in different individuals, or, more usually, in the form of a color pattern, made up partly from one base and partly from the other (each being clearly defined) in the same individual.

Some mosaic species, such as *Tropiometra afra* and certain of the Comasteridæ are peculiar in that some specimens belong exclusively to type I (yellow) and others exclusively to type II (violet) but none are ever mixed.

The mosaics are, the Zygometridæ, the Comasteridæ, the Thopimetridæ except Asterometra, Iridometra, Antedon, Erythrometra, Perometra, Hypalometra, Promachocrinus, and the Himerometridæ.

The data seem to show that the smaller stalked forms are invariably and unchangeably yellow, which color may be, as in the case of the parrots among birds, equivalent to a lack of color. Black is added to the basic color of comatulids at all depths, and appears to denote age. Blue is added apparently only within 200 fathoms of the surface, and increases in intensity to the surface. The mosaics are all littoral or shallow water types.

Species growing among coral or on white bottoms in shallow water are very dark in color, often nearly black or sharply black and white, while the same species on mud may be light yellow and pinkish; or a species may be purple and yellow in comparatively deep water, and violet and white in shallow water. We seem to be able to trace a close connection between color and amount of illumination, the blue factor in the coloration increasing with the light.

There appears to be no direct relation between the color of crinoids and their environment. The yellow deep water species are very conspicuous in the mud from a deep dredge haul, while the color of shallow water species, as just indicated, is commonly in great contrast to their surroundings. Crinoids can have little to fear, because their extremely calcareous organization would seem to make them very undesirable as food; on the other hand, a strongly contrasting coloration might be of advantage in attracting small organisms, as contrast spots on flowers do insects; observations in this point would not be difficult to make, and might lead to interesting results.

The other echinoderm classes appear to be in general subject to the same laws of color change as the crinoids, but the records are much more complete and satisfactory, and the specimens are not so much changed in preservation. They would, therefore, offer an interesting field for study.

These are some of the more interesting inferences to be deduced from an examination of the literature on the Crinoidea in its present state; and, in view of the great geological importance of the group, and its bearing on important geologic problems, it is to be hoped that this phase of the subject, as well as the systematic and anatomical sides will in the future receive its due attention.

SHORTER ARTICLES AND CORRESPONDENCE

EVOLUTION WITHOUT ISOLATION

Is isolation a factor of evolution? The answer must depend, obviously, on what we mean by evolution, as well as upon the relations of the facts. Every difference of opinion regarding the nature and causes of evolution involves the use of the word in a different sense, unless the process is to be renamed with each change of interpretation. The choice of words is worthy of careful consideration, but words should not lead us away from the broader issue of biological facts. The practical question is not whether the words or their senses are new or unusual, but whether the facts are correctly represented.

Being convinced that changes in the characters of species are spontaneous, I apply the word evolution to these spontaneous processes of change. This, of course, is not the meaning of those who believe that changes in species are brought about by external influences working upon normally stationary groups, who have been accustomed to think of evolution as a passive result of change in the environment, rather than as an active process, inherent in the species.

From one point of view evolution appears as a complex of different kinds of environmental influences, from the other as a process of growth in the species, somewhat analogous to the development of individual organisms of which species are composed. In the one case the species are thought of as being carried or pushed along by their environments, in the other as advancing by motions of their own, often in spite of environmental obstacles and deflections.

Belief in isolation as a factor of evolution marks an intermediate stage of opinion between those who hold that natural selection causes evolution, and those who reject selection as a cause. The effort is to maintain the doctrine of environmental causes by giving selection the assistance of other alleged factors, such as isolation, mutation, environmental variation, heredity, ontogeny, etc. Nevertheless, this course has its logical dangers for the theory of selection, for the placing of much emphasis on isolation is practically equivalent to saying that evolutionary

changes go on of themselves, without the need of environmental interference.

If we advance with sufficient confidence in isolation we eventually come through to the realization that our alleged environmental factors are unnecessary as causes, because evolution is spontaneous. This approximation of views has been recognized by Dr. John T. Gulick who states in the January number of the AMERICAN NATURALIST that our interpretations differ only in the meaning attached to the word evolution.[1]

I am naturally very much pleased to agree with Dr. Gulick, for no other student of isolation has given the subject such extensive and thorough study. I subscribe to Dr. Gulick's statement that there does not seem to be any essential difference between us regarding facts. The difference is that the facts appear to me as of more significance than Dr. Gulick has represented. In attempting to point out this greater significance I have used a different method of expression.

To say that isolation and selection are factors of evolution should mean, in simpler English, that they cause evolution, or at least help it along, whereas they do neither. They appear to cause or to conduce to evolution only so long as we take it for granted that changes in the characters of species are dependent upon the subdivision of species, to form additional species.

The separation of a species into two or more parts allows the parts to become different, but there is every reason to believe that evolutionary changes of the same kind would take place if the species were not divided. That the isolated groups become different does not indicate that isolation assists in the process of change. It gives the contrary indication that changes are restricted by isolation. If isolation did not confine the new characters to the groups in which they arise, the groups would remain alike, instead of becoming different. Thus it appears to me that the danger of confusing the issues is much greater when we say that isolation and selection *are* factors of evolution, than when we say that they are *not* factors of evolution, however important they may be in multiplying and differentiating species.

Sufficiently narrow forms of isolation no doubt affect plants and animals in nature in the same way as the "intensive segre-

[1] Isolation and Selection in the Evolution of Species. The Need of Clear Definitions. *The American Naturalist*, 42: 48, January, 1908.

gation'' by which domesticated types are induced to change some of their characters, but it does not appear that this intensive segregation is a condition of evolution. Differences between small groups are more obvious and more readily definable because small groups are generally more uniform, like the pieces with uniform patterns which may be cut from a variously figured fabric. Isolation is the shears that splits the species, not the loom that weaves it. The weaving is done when the fabric is broad. The larger and more diversified species make the truly constructive evolutionary progress.

The evolution of a species is in no way dependent upon its being split into smaller groups, but is more likely to be hindered by narrow subdivisions. If the groups are too small they degenerate and become extinct, instead of continuing their evolution. Isolation, though making more species, impedes evolution. In like manner, selection favors adaptation, because it keeps species from evolving in non-adaptive directions. Isolation and selection may still be considered as evolutionary factors if this time-honored reckoning is too sacred to be changed, but they must stand as negative factors instead of positive, if my interpretation is correct.

Darwin saw in his later years that evolution is not altogether the same as the formation of new species, and used in a letter (published after his death), the word ''specification'' as a means of expressing this distinction, a suggestion which I unwittingly repeated in proposing the slightly different word ''speciation.''[2]

> There are two different classes of cases, as it appears to me, viz., those in which a species become slowly modified in the same country (of which I can not doubt there are innumerable instances) and those cases in which a species splits into two or three or more new species, and in the latter case, I should think nearly perfect separation would greatly aid in their "specification," to coin a new word.[3]

Darwin was concerned to show that species multiply and diverge in nature, for this is good evidence of the general fact of evolution. Nevertheless, it should not be assumed that all forms of divergence represent evolution, or that divergence is a true measure of evolution. Divergence may be less than evolution, for the evolutionary paths of related groups often follow

[2] Factors of Species-Formation, *Science*, N. S., 23: 506.

[3] Life and Letters of Charles Darwin, 2: 339. New York, 1896.

nearly parallel directions. Divergence may be greater than evolution when changes are not progressive but sideways or backwards. Mutations, reversions, or degenerations, can take place suddenly, without the slow and gradual weaving of new characters in the network of descent of a species; they involve only the suppression of characters or the return to expression of old characters that continue to be transmitted in latent form.

As long as Dr. Gulick lets it appear that the divergencies of his snails arise through isolation, I fully agree with him, but not when he seems to suggest that isolation and selection produce new characters. The fact that isolated groups have no mutual sharing of evolutionary progress leaves them free to become more and more different, but the isolation does not explain the progressive changes to which the differences are due. Isolation explains *speciation,* but does not explain *evolution.*

This is the same objection that Darwin made to Wagner's theory of isolation, that it did not help him to understand "how or why it is that a long isolated form should almost always become slightly modified." Dr Gulick explains that his interpretation differs essentially from that of Wagner, who held that even natural selection must have an "isolated colony" to work upon. Nevertheless, it appears that Darwin's objection applies to Gulick's doctrine as well as to Wagner's, for isolation only reveals the fact of evolution, while a genuine "factor" should do something toward explaining it.

Such a factor Darwin believed that he had found in natural selection, but he saw in isolation alone nothing to aid evolution. Darwin took it for granted that species were *normally stationary* and most of his successors still accept this unevolutionary assumption. With Darwin evolution was a definite process by which the characters of a species are changed, but with some of our later writers it has become merely a general name for a subject of study, whose various phases or branches are loosely called "factors," though they have no apparent relation to the original concrete idea of evolution as a process of change in species.

The failure to give a more definite recognition and a name (evolution or otherwise) to the processes of spontaneous, progressive change in species, appears to me to have prevented the attainment of the complete clearness sought by Dr. Gulick in the presentation of his elaborate and valuable evidence that only

isolation is needed for evolutionary divergence to become manifest. If Dr. Gulick really agrees with me that evolution is spontaneous, I must submit that his adherence to the custom of treating isolation and selection as factors has served to conceal his conclusions, rather than to announce and defend them.

O. F. Cook.

Washington, July 16, 1908.

A NOTE ON THE SILVERSIDE

In view of its value as a food fish, and as food for other more valuable fishes,[1] the following note on the habits of the silverside has special interest.

At Chesapeake Beach, Md., April 19, 1908, p. m., the tide was rising and probably pretty well up. At points where weed and such riff raff was partially buried in the beach, in the wash of the ripples which followed one another in, numerous fishes were wiggling actively as though stranded. At times one would be almost or quite clear of the water, but so active were they that the writer, not having a net, was at first unable to capture any. They evidently knew what they were doing, as when a spot they occupied was approached, they disappeared from it. Finally, by striking quickly with a piece of wood at a place where some were congregated, three were disabled and secured, which proved, as anticipated, to be *Menidia menidia.*

Examination of a specimen of beach trash collected where the fishes were observed, at the time, shows the presence of a number of eggs, apparently of *Minidia,* strong evidence that the fish were spawning. These eggs are one mm. or a little more in diameter and bear filaments at one point which attach them to the beach material in which they occur more or less scattered. The white color of the egg (preserved in alcohol) is relieved by yellow oil masses. This spawning ground, if such it was, would certainly be exposed at low tide. The species, in this case its northern race, has previously been noted to spawn above low-tide level.[2] Chesapeake Bay is neutral ground between the northern and southern races of *Menidia menidia,* and the writer prefers to refer the specimens obtained to neither race.

John Treadwell Michols.

U. S. Bureau of Fisheries.

[1] W. C. Kendall. U. S. Fish Comm. Rept., 1901 (1902), p. 241.

[2] H. C. Bumpus, *Science,* N. S., Vol. VIII, No. 207, p. 851, Dec. 16, 1898.

NOTES AND LITERATURE

BOTANY

The Origin of a Land Flora.[1]—Speculations concerning the origin of the higher plants have always had a special attraction for the botanical student whose work extends beyond the limits of mere collecting and tabulation. Perhaps the very fact that we can never expect to discover all of the factors concerned with the evolution of the vegetable kingdom, and that our conclusions are always liable to be materially altered through the discovery of new facts, or a different interpretation of those already known, gives an added zest to the hunt for new forms or the discovery of new facts about those already known which may add another stone to the edifice which is being slowly built up.

The volume under consideration is one deserving more than passing attention from the student of plant evolution. Not only is it the work of one of the keenest investigators of some of the most difficult problems with which the botanist has to deal, but the book represents the fruits of many years' arduous labor, but evidently a labor of love, which has yielded results of the utmost importance and provides a mine of accurate information, presented in an unusually clear and attractive style. From a literary standpoint, it might well be recommended as a model to some of our scientific writers who, it must be confessed, do not always compare very favorably with their English colleagues in the matter of literary form.

Aside from the wealth of facts brought together in this handsome volume, illustrated by many admirable illustrations, the reader constantly encounters speculations, sometimes almost startling in their originality, with which he may not always agree, but which are certain to set him thinking deeply; and we believe that this book will be a great stimulus to the further exploration of many obscure, but very important, questions bearing upon the affinities of the higher plants.

[1] The Origin of a Land Flora: A Theory based upon the Facts of Alternation. By F. O. Bower, ScD., F.R.S., Regius Professor of Botany in the University of Glasgow. Pp. xi + 727, many illustrations. New York, The Macmillan Co.; London, Macmillan and Co., Limited. $5.50 net.

It is not necessary to remind botanists of the high standing of Professor Bower's numerous contributions to science. Not only has such work as his great monographs on spore-producing organs put him in the first rank of morphologists, but his interpretation of the facts of comparative morphology, and his more speculative papers on alternation of generations and the origin of the land plants, have strongly influenced all recent theories on these important questions. Professor Bower is thus peculiarly fitted to treat this difficult subject, and it is with special gratitude to the author that botanists will welcome this admirable presentation of the results of his many years' labors.

It is generally admitted that the existing land flora, *i. e.*, the Archegoniatæ and seed plants, are the descendants of some fresh-water plants probably allied to certain green algæ; but the way in which these typically aquatic organisms gave rise to forms markedly terrestrial in habit is one of the questions about which there are very diverse opinions. Professor Bower has long contended, and we believe that he has overwhelming evidence on his side, that the characteristically terrestrial modern plant type, *i. e.*, the sporophyte or neutral generation of the ferns and seed plants, is the product of the evolution of the zygote or resting-spore of some fresh-water algal type, the result of the union of the sexual cells, or gametes, and in most cases is an adaptation to surviving periods of drought to which these plants are liable. That is, the sporophyte is from its inception a terrestrial or subaerial phase interpolated between the active aquatic growth periods. This is the "antithetic" theory of alternation, and it is this thesis, opposed to the "homologous" alternation which of late has been defended by a number of eminent botanists both at home and abroad, that Professor Bower defends in the present volume.

In his previous work, Professor Bower has elaborated his theory of the important part that the sterilization of potentially sporogenous tissue has played in the evolution of the sporophyte of the higher plants. Particularly has he made this clear in his important series of monographs on the development of the spore-producing organs of the Pteridophytes. The present volume is divided into three parts: (1) The Statement of the Working Hypothesis, (2) Detailed Statement of Facts, (3) Conclusion.

It has been rather the fashion of late to belittle the importance of comparative morphology, as it is evident that the plant organ-

ism, with its potentially unlimited power of regeneration and growth, is extremely plastic and responds promptly to any external stimuli. Nevertheless, the facts of comparative morphology are too evident to be ignored, and although the modern student must carefully check his work by the data furnished from experimental morphology, physiology, and paleontology, it still is evident that the surest clues to relationship must be sought in a comparison of corresponding structures and the facts of ontogeny.

The phenomena of alternation of generations as exhibited by the higher plants are familiar to the botanist. The plant shows two marked life phases, first the sexual phase, or gametophyte, and second the neutral generation, arising from fertilization, the sporophyte. In all but the highest plants, the seed plants, the gametophyte betrays more or less clearly its aquatic origin. It is usually poorly adapted to resist dryness. Water is necessary for fertilization, as the male gametes are ciliated and the mature sexual organs require water for their proper dehiscence. In the lower types, like the simple liverworts, the gametophyte is relatively larger and plays a much more important rôle in the plant life than does the insignificant sporophyte, which is short-lived and dies as soon as it has shed its spores, whose production is the aim of its existence. The sporophyte in the lower forms is never an aquatic structure, but receives its water indirectly from the gametophyte with which it is permanently in intimate association.

With the increasing specialization of the Archegoniates, several lines of development were inaugurated showing several different types of specialization both in the gametophyte and in the sporophyte. The gametophyte reaches its culmination in the higher mosses which seem to show the limit of the possibility of adapting the essentially aquatic gametophyte to life on land. The further development of the land plants is therefore bound up with the elaboration of the terrestrial phase of the plant's life history, *i. e.*, the sporophyte. With the increasing importance of the latter there is a progressive reduction of the gametophyte which culminates among the Pteridophytes in the extremely reduced gametophytes of the heterosporous forms like Marsilia or Selaginella.

It is not likely that any existing liverworts represent very nearly the direct ancestors of the Pteridophytes or "Vascular

Cryptogams." It may be said, however, that some remarkable parallelisms, if not real homologies, are shown by the peculiar Anthocerotes, and there is a progressive development of the sporophyte in both liverworts and true mosses which hints at least at the course of evolution which finally resulted in the entirely independent sporophyte of the ferns. The evolution of the sporophyte consists in a constantly increasing development of sterile or non-sporogenous tissues, which assume the character of green assimilative tissue, etc., and it may finally develop definite external organs, roots and leaves, the former connecting the sporophyte with the earth and making it quite independent of the gametophyte. Finally, spores are produced, always in a perfectly uniform manner in groups of four, and the life history is complete.

While only a relatively small number of forms have been investigated, it is pretty certain that the sporophytic tissues normally have nuclei with twice the chromosome number found in the cells of the gametophyte, this being the result of the doubling of the chromosomes due to the fusion of the gametes. The reduction of the chromosomes occurs in the tetrad division resulting in the spores, which therefore possess the normal gametophyte number.

The formation of the sporophyte by apogamy or direct budding from the prothallium, and the various buddings of the gametophyte from the leaves of the sporophyte, are the strongest arguments in favor of "homologous" alternation; but the facts of apogamy and apospory may be explained as cases of adventitious budding analogous to so many cases found in the seed plants, and much more evidence is needed to show that they are normal rather than pathological.

Comparing the sporophytes of the Bryophytes and Pteridophytes, the latter are distinguished by the development of external organs. A more or less conspicuous central axis has appendicular organs, leaves, roots and sporangia, the latter being the characteristic organs which distinguish the different types of vascular plants. They may be supposed to have arisen from the more or less complete segregation of masses of sporogenous tissue from the originally continuous layer of some such form as Anthoceros. The gradual evolution of the sporangium from the large indefinite sporocysts like those of Ophioglossum to the very definite sporangia of the highly

specialized leptosporangiate ferns can be clearly followed in existing types. Professor Bower does not regard the Ophioglossales as related to the true ferns, but from this view we feel obliged to dissent.

As might be expected, much stress is laid upon the "Theory of the strobilus" with which Bower's name is especially associated. This theory assumes that from some bryophytic sporangium, perhaps not very different from that of Anthoceros, by the segregation of definite sporangia each subtended by a leaf-like organ originating from the sterile tissue between the sporangia, a cone or strobilus would be derived, *i. e.*, an axis upon which are borne a number of leaves usually spirally arranged, each one subtending a sporangium. This condition is still met with in some of the simple species of Lycopodium like *L. selago* and it is an extremely ancient one.

This theory of the strobilus when applied to the Lycopods has very much in its favor, and is certainly the most plausible explanation yet put forward as to the origin of the Lycopods; but is not so convincing when one tries to reduce the ferns also to the strobiloid type. It is true that in the Cycads, which are doubtless of fern affinity, a strobilus is present, but there is very strong reason to suppose that it is a secondary condition.

The chapter on "Embryology and the Theory of Recapitulation" is a very sane treatment of an extremely difficult problem. While recognizing that the first students of vegetable morphology went much too far in their insistence upon the importance of the exact succession of cell divisions in the young embryo in their relation to the subsequent organs of the plant, nevertheless it is unquestionable that the early divisions of the embryo are to a certain extent a recapitulation of the early phylogeny. It must be remembered that the young embryo has been subjected for countless ages to practically the same conditions, and that under these conditions certain definite early segmentations should be fixed is merely what would be expected. One of these conditions is the action of gravity and this beyond question is the most important factor in determining the marked polarity of the embryo. As to the general application of the theory of recapitulation to the later stages of development, as Professor Bower very well points out, great caution has to be used, but nevertheless within proper limits it is justified.

Professor Bower maintains that there is but one type of leaf.

All leaves, he thinks, are primarily sporophylls. Foliage leaves are reduced sporophylls and cotyledons, and "protophylls" mere modifications of the foliage leaves. This is not, however, a view that can be accepted without some qualification. While undoubtedly on the theory of antithetic alternation, spore-bearing structures must have preceded foliage leaves, it may be questioned whether these primary spore-bearing structures at least in the case of the Ophioglossaceæ and Equisetaceæ, were not rather of the nature of sporangiophores than sporophylls in the strict sense of the word. If such is the case, the sterile leaves would be outgrowths of the sporangiophores, or even independent structures rather than direct metamorphoses of sporophylls.

From a study of the anatomical evidence, the conclusion is reached that the primitive state in the Pteridophytes was one in which the axis was structurally dominant in the shoot, and the type of cauline bundle a solid monostele. It is also concluded that the bipolar, radially symmetrical condition of the sporophyte is more ancient than the dosi-ventral condition.

The problem of the origin of the roots of the vascular plants by means of which the independence of the sphorophyte is finally secured is recognized as a very difficult one. In some Lycopods no root is formed in the embryo until after several leaves have been developed, and the name "protocorm" has been proposed for this early undifferentiated plant-body, the assumption being made that it represents an ancient condition antedating a plant-body with true leaves. Professor Bower, however, is inclined to doubt the accuracy of this hypothesis.

While recognizing the great value of the evidence of paleophytology, and the important contribution that the study of fossils has made to our knowledge of the evolutionary history of the Pteridophytes it is pointed out how very little light has been thrown by this science upon such fundamental questions as the origin of the bryophytic sporogonium or that of the leafy sporophyte.

In chapter nineteen are discussed the difficulties of determining whether amplification or reduction has been the more important factor in determining the course of evolution in certain cases. Chapter twenty contains a succinct summary of the Working Hypothesis and concludes Part I.

Over 400 pages of text with many admirable illustrations are devoted to Part II, "A Detailed Statement of Facts." This is

an excellent account of the sporophytic structures of the Archegoniates and would by itself form an important volume. As might be expected in a treatise on land plants, and from the author's previous works, the Pteridophytes are the principal subjects of study, only two chapters out of twenty being devoted to the Bryophytes. Space forbids even an outline of the great mass of facts brought together, not the least interesting and important being those derived from a study of the fossil forms which of late have attracted so much attention. Very little space is given to the study of the gametophyte, and while no doubt in the problem of the origin of a land-flora the sporophyte is much the more important factor, still we can not but feel that in some cases, a careful study of the gametophyte would have resulted in some different conclusions and would have served as a useful check. Thus all the recent work on the gametophyte of the Ophioglossaceæ emphasizes the strong similarity in the reproductive organs of these forms and those of the Marattiaceæ and makes more probable than ever a real relationship existing between these two orders of eusporangiate ferns.

There are recognized three phyla or main developmental series of Pteridophytes, the Lycopods, the "Sporangiophoric Pteridophytes" and the ferns, excluding from the latter the Ophioglossaceæ which Professor Bower thinks at present had best be treated as a fourth phylum, although he concludes that there is good evidence of a more or less evident affinity with the "Sporangiophoric Pteridophytes."

The isolated position of the Lycopods is recognized by Professor Bower, and there certainly is very strong reason, both from a study of the gametophyte and sporophyte, for assigning to this group an origin quite apart from that of the other Pteridophytes.

The most radical departure from the ordinarily accepted arrangement of the Pteridophytes is the establishment of the group of "Sporangiophoric Pteridophytes" which includes the Equisetales and the fossil Sphenophyllales with which latter group are included the anomalous Psilotales, which have usually been associated with the Lycopods, but whose isolated position has for some time been clearly recognized. To the sporangiophoric Pteridophytes Bower also thinks the Ophioglossales may be related. The sporangiophore is defined as a more or less elongated vascular stalk upon which sporangia are borne. The sporangiophores are considered to be organs *sui generis* not a

modification of either a foliar or cauline organ. The question is left open whether the sporangiophore is to be regarded as the elaboration of a single sporangium, like that of Lycopodium, but it seems to us that the origin of the sporangiophore as a compound structure from the beginning, is more in harmony with the facts of comparative anatomy.

The acceptance of this view will we believe help to solve some of the most puzzling questions as to the affinity of the primary pteridophytic stocks. While convinced of the real affinity between the Ophioglossaceæ and the true ferns, we have also more than once called attention to the marked resemblance between the gametophyte of Equisetum and that of the lower ferns; and it may be added that there are also correspondences in the embryo that are probably not without significance. If then we admit that the sporangiophoric Pteridophytes really represent a natural division of the Pteridophytes, it is quite conceivable that from some common ancestral form having a large green gametophyte like that of the lower ferns, two types of sporangiophoric sporophytes may have arisen, one developing the strobiloid group of sporangiophores, as in Equisetum, the other a single large sporangiophore like that of Ophioglossum. There is very good reason to suppose that the sporangiophore of the Ophioglossaceæ is not an appendage of the so-called sporophyll, but is a quite independent organ, the sterile lamina being rather an appendage of the sporangiophore than the reverse.

In spite of Professor Bower's argument we can not but feel that the resemblances between the Ophioglossaceæ and the true ferns are too numerous and exact to be explained on any other ground than that of a real affinity; but this does not lessen the importance of his explanation of their probable affinity with the Equisetales and Sphenophyllales.

The classification of the Filicales excluding Ophioglossaceæ is that already elaborated in his memoirs on spore-producing members. Three groups of the Filicales are recognized. One, Simplices, in which all of the sporangia of a sorus are formed simultaneously. Two, Gradatæ in which there is a definite success in time and space; and Three, the Mixtæ in which there is a succession in time but not in space. Six families are included in the first group. The Botryopterideæ (fossil), the Marattiaceæ, Osmundaceæ, Schizæaceæ (Marsiliaceæ)? Gleicheniaceæ and Matonineæ. The Gradatæ include five families. Lox-

somaceæ, Hymenophyllaceæ, most Dicksonieæ, Dennstædtiinæ, Cyatheaceæ (Salviniaceæ)? The remaining families often grouped together as Polypodiaceæ form the group of the Mixtæ.

The Botryopterideæ comprise some of the earliest known fossil Filicales. Their affinities, however, are somewhat obscure, and the group seems to have been a synthetic one. They show certain evidences of affinity with the Marattiaceæ also with the Osmundaceæ and Hymenophyllaceæ. It might also be suggested that a comparison of the sporangium might be made with Botrychium and perhaps Helminthostachys.

We must pass over with brief mention the very detailed account of the ferns which occupies over 150 pages of the text. The tendency in the evolution of the sporangium is very clearly from the larger eusporangiate type of the Marattiaceæ reaching its maximum in Kaulfussia, where nearly 8,000 spores occur in the single sporangium, to the numerous, small leptosporangiate sporangia of the Mixtæ where there may be only from 8 to 64 spores. It may be added that the sporangia of Ophioglossum represent a still more primitive type, both in their large size, their indefinite limits and very great number of spores.

The assumed relation of the different families of the Filicales is graphically shown in the diagram on page 653.

Part III is a summary covering some sixty pages. The most important conclusion may be briefly stated as follows: "*Certain Algæ suggest in their post-sexual phase how the initiation of a sporophyte may have occurred, but there is no sufficient reason to hold them as being in the actual line of descent of archegoniate forms.*" "*Both Mosses and Liverworts may with probability be held to be blind branches of descent,* which illustrate nevertheless phyletic progressions that illuminate the origin of sterile tissues from those potentially fertile, and the establishment of a self-nourishing system in the sporophyte." "*It may accordingly be concluded as probable that the prothallus of early Pteridophytes at large was a relatively massive green structure, with deeply sunk sexual organs.*"

The Lycopodiales stand by themselves in the simplicity of the sporangial arrangement and constitute a type of extreme antiquity, which has come down practically unaltered to the present day. Their comparative study may be conducted independently of other phyla: for there is no reason to think that they were derived from any other known vascular type. . . . *The condi-*

tion actually seen in the 'Selago' type may be held as truly primitive, and Lycopodium Selago, *with its imperfectly differentiated shoot, is in fact a near approach in a living species to the ideal primitive form which emerges from wide comparative study of the phylum as a whole.*"

"*The functionally identical parts designated sporangiophores and sporangia are cognate parts; it appears probable that the sporangiophore is itself a consequence of elaboration of a simpler type of spore-producing member, of which the sporangium of* Lycopodium *is an example, while the trabeculæ in* Isoetes *and* Lepidostrobus Brownii *suggest a mode of origin of the septate state. If this were so, then the sporangiophore would have been distinct in its phyletic origin from the bract-leaves, which habitually subtend the spore-producing members, whether they be sporangia or sporangiophores.*"

"*The phyletic relationship of the Sphenophyllales and Equisetales has undoubtedly been a very close one; the distinguishing features are not to be found in the primary plan or construction of the shoot, so much as in the secondary modifications of number and relation of the appendages, and of their branching, together with changes in the originally protostelic structure of the axis. Such considerations support the conclusion that the Sporangiophoric Pteridophytes constitute a brush of naturally related phyletic lines.*"

The Ophioglossales are regarded as an ascending series of forms the "*spike illustrating various steps in the increasing complexity of a body of the nature of the sporangiophore.*" "The whole unbranched shoot is a single strobilus bearing leaves of which all are potentially fertile and the majority actually so." "*The Ophioglossaceæ appear to have been an upgrade sequence, sprung from some sporangiophore stock, and bearing no near relation to the large-leaved ferns.*"

"*The Filicales were ultimately of strobiloid origin, but have undergone amplification of their leaves analogous to, but phyletically quite distinct from what is seen in other Pteridophytes, and carried to a higher degree.*"

"One chief reason for regarding the lines of the Filicales and Ophioglossales as distinct lies in the difference of position of the spore-producing members. It has been argued above (p. 633) that the soral condition was primitive for ferns, and that *the sorus is a body similar in kind to the sporangiophore, the two*

being alike in function, in structure, and in capacity for fission and extension: the number and position are points of difference."

The Filicales are considered to be a phylum showing fundamentally the strobiloid characters, but secondarily modified in relation to their pronounced megaphyllous habit. *"Accordingly, the Filicales appear as the most divergent phylum of homosporous Pteridophytes."*

"Comparison of the several phyla, as represented both by their fossil and their modern representatives, leads in each case towards the recognition of a primitive type, and its construction in the several phyla has certain features in common. The chief of these are the definition of axial polarity in the first initiation of the embryo: the continued apical growth; the radial construction of the shoot: the origin of the appendages laterally from the axis by enation, and in strictly acropetal order: a protostelic structure of the conducting system of the axis, and a leaf-trace composed of a single strand."

"The sporophyte . . . probably arose originally as a structure of limited size, and unbranched, upon a prothallus of considerable dimensions, and producing *Homosporous Spores.*"

"The adoption of *Heterospory,* and of the *Seed Habit* supervened later. This, while it has led to the final independence of the land flora as regards external fluid water for the completion of its life-cycle, has brought as a secondary consequence a widespread reduction."

"The final goal of all organic development is the establishment of new individuals. The evolutionary story of the sporophyte illustrates this in two distinct ways. *In the prior and non-specialized homosporous forms large numbers of germs are produced: . . . consequently amplification of the whole sporophyte is the leading characteristic of these earlier types; . . . In the later and more specialized heterosporous forms and particularly in the Seed Plants with their more refined methods, individual precision supersedes mere numbers; and reduction of the propagative system has been its usual concomitant."*

"The sporophyte, which is the essential feature in the Flora of the Land, is referable back in its origin to post-sexual complications: *it appears to have originated as a phase interpolated between the events of chromosome-doubling and chromosome-reduction in the primitive life-cycle of plants of aquatic habit."*

DOUGLAS HOUGHTON CAMPBELL.

PLANT CYTOLOGY

Apogamy in the Ferns.—It has long been known that the archegonia in a number of ferns are not functional and that in these forms the sporophyte generations arise as vegetative outgrowths from the gametophytes. This suppression of sexuality with the development of the succeeding generation asexually is termed apogamy. Only recently, however, have there been any cytological investigations of the phenomenon.

Farmer and Digby[1] were the first to study the nuclear behavior throughout critical phases in the life history of apogamous ferns. The results, based on forms of Lastrea, Athyrium, and Scolopendrium, led these authors to describe three conditions.

1. The process of sporogenesis is omitted from the life cycle in three varieties of *Athyrium Filix-fœmina* and in a form of Scolopendrium giving the condition of apospory known for a number of ferns. The prothallia arise directly from abortive sporangia or from pinnæ; the sporophytes develop apogamously from the prothallia or from unfertilized eggs; and the approximate number of chromosomes is retained throughout the life cycle. This type of life history brings apogamy into close association with apospory. The omission of the process of chromosome reduction, characteristic of sporogenesis, gives the gametophytes the sporophytic number of chromosomes (2x). Apogamy seems to be a natural consequence, for gametes would not be expected to function under such conditions since they would double the number of chromosomes with each nuclear fusion and there would be no reduction divisions to bring the higher numbers back to the normal. These conditions in the ferns agree with certain cases of apogamy among the seed plants (*Antennaria alpina*, *Thalictrum purpurascens*, and apogamous species of Alchemilla and Hieracium) where the reduction mitoses are omitted in the ovule and the nuclei of the embryo sacs contain the sporophyte number of chromosomes, the embryo developing from unfertilized eggs or even from synergids. The most interesting feature of this type of life history is the development of gametophytes with the 2x or sporophytic number of chromosomes, showing that the morphology of this phase in

[1] Farmer, J. B., and Digby, L. Studies in Apospory and Apogamy in Ferns. *Ann. of Bot.*, XXI, p. 161; 1907.

the life history does not depend upon its containing the reduced number.

2. In *Lastrea pseudo-mas* var. *cristata apospora* apogamy and apospory follow one another in the same manner as described above, but the number of chromosomes (probably 60) is so close to that of the gametophyte in the type species (72) that it seems probable that in this form the sporophyte retains the reduced number (x) of the gametophyte. This condition is exactly the reverse of that noted above showing that the morphology of the sporophyte likewise does not depend upon its containing the double number (2x) of chromosomes.

3. The third and most striking conditions described by Farmer and Digby refer to a peculiar migration and fusion of nuclei in the cells of the prothallium just before the apogamous development of the sporophytes. These observations are recorded from the study of two *polydactyla* varieties of *Lastrea pseudo-mas* which form their spores with chromosome reduction in the usual manner. The nuclear migrations and fusions occur in the younger regions of the prothallia, in the wings as well as in the thicker portions. A nucleus assumes an elongated form with the pointed end against the wall which it is about to pierce. A pore is formed through which the nucleus slips and makes its way to the nucleus of this receptive cell which usually remains rounded. The two nuclei come to lie closely pressed against one another and gradually fuse. Older prothallia thus have fusion nuclei with double the gametophytic number of chromosomes (2x) and the cells of the apogamously produced sporophytes are found to have nuclei of this type; the authors conclude that they are derived from such fusion nuclei. This process of migration and nuclear fusion, taking the place of the fusion of gametes, finds its analogy in the recent studies of Blackman and Christman on the rusts. Just previous to the development of the æcidia there is an extensive migration of nuclei between neighboring cells so that the cells which give rise to the chains of æcidiospores contain conjugate or paired nuclei, the descendants of which remain in pairs until the nuclear fusion in the teleutospores. Thus in the rusts and in these ferns a process of nuclear fusion concerned with vegetative cells has apparently become substituted for the fusion of gametes which are no longer functional.

The most recent cytological contribution to the study of apogamy in the ferns is by Yamanouchi.[2] This paper gives a much more detailed account of nuclear structure and the behavior of chromosomes than that of Farmer and Digby, and is remarkable for the thoroughness of the study of critical phases throughout the entire life history. We have already noticed a portion of the work in the review of some recent research on cilia-forming organs of plant cells in the August number of the NATURALIST. Yamanouchi worked upon *Nephrodium molle* which has the advantage of presenting under ordinary conditions of culture the normal life history of ferns. The apogamous development of sporophytes may, however, be readily induced in prothallia exposed to direct sunlight and watered from below so as to prevent the possible escape of sperms and fertilization of archegonia. Such prothallia develop much more slowly than under normal conditions. After six weeks the cushion regions become markedly thickened, which thickenings indicate the beginnings of apogamous sporophytes.

Yamanouchi made very accurate counts of the chromosomes throughout the critical phases of the normal life history preliminary to a comparison with apogamous conditions. The chromosome number in the sporophyte is 128 or 132, which is reduced during sporogenesis to 64 or 66 in the usual manner. The gametophyte has then 64 or 66 chromosomes which were counted in the vegetative cells of the prothallia and in the mitoses leading up to the formation of sperms and eggs. The fertilized egg has of course the double or sporophytic number.

Prothallia, which under the culture conditions described above produce sporophytes apogamously, have 64 or 66 chromosomes. The mitoses up to the 30–50 cell stages are similar to those in normal prothallia. After that the growth is very slow and there are irregularities in the position of the cell walls with reference to the surface of the prothallia. The apogamous prothallia produce antheridia in abundance which develop motile sperms, the mitoses showing 64 or 66 chromosomes. Archegonia are, however, rarely formed on apogamous prothallia. Occasionally archegonia initials are differentiated, from which a central cell is cut off as in normal prothallia, but this central cell either remains undivided or produces eggs and canal

[2] Yamanouchi, S. Apogamy in Nephrodium. *Bot. Gaz.*, XLV, p. 289, 1908.

cells in an archegonium with a poorly developed neck; it is doubtful whether such eggs are capable of being fertilized.

The sporophytic outgrowths on apogamous prothallia arise coincident with the development of the cushion region. Superficial cells on the underside increase in size, and from one of these an apical cell is cut off which becomes the growing point of a leaf. Meanwhile there is a rapid division of the neighboring cells in the interior so that an area of meristematic tissue results which gives rise to the young sporophyte in direct connection with the prothallial cells. A leaf and stem axis are developed from two superficial apical cells, the root tip arises endogenously, scalariform vessels appear in the tissue connecting the developing leaf and stem, and finally there is differentiated the young sporophyte with root, stem and leaf regions. Mitoses are easily found in stages of this apogamously developed sporophyte and always show 64 or 66 chromosomes, the gametophytic number of the prothallium. Consequently, in *Nephrodium molle*, there is no doubling of the number of chomosomes in the development of apogamous sporophytes through nuclear migration and fusion as described by Farmer and Digby for the *polydactyla* varieties of *Lastrea pseudo-mas*. It has not yet been determined whether these apogamous sporophytes develop spores.

Apogamy in Nephrodium, therefore, presents conditions different from anything as yet recorded for plants, since following normal sporogenesis a sporophyte is developed with the gametophytic or haploid number of chromosomes (x), and there is no place in the life history for the diploid or sporophytic number. The case of *Lastrea pseudo-mas* var. *cristata apospora* is apparently not the same since in that form apogamy follows apospory. However it is possible that the apogamous sporophytes of Nephrodium may be found at maturity to develop apospory and thus swing into a type of life history similar to that recorded by Farmer and Digby for the above form of Lastrea. The most significant results of Yamanouchi's investigation is the clear evidence that the morphology of the sporophyte does not demand that its cells contain nuclei with the double or diploid number of chromosomes (2x), in other words that the "number of chromosomes is not the only factor which determines the characters of the sporophyte and gametophyte," a conclusion indicated by the known cases in both ferns and seed plants

where gametophytes have the sporophytic number of chromosomes.

A third paper which should be mentioned in connection with these two on types of homosporous ferns is Strasburger's[3] study of apospory in heterosporous Marsilia. Parthenogenesis had been reported by Shaw as occurring in 50 per cent. of the female gametophytes of *Marsilia Drummondii.* Nathansohn had induced parthenogenesis in *Marsilia vestita* and *M. macra* by keeping germinating megaspores at a temperature of 35° C. for 24 hours and then allowing them to continue their development at a temperature of 27° C. Under this treatment the eggs of 7–12 per cent. of the spores gave rise to embryos parthenogenetically while at lower temperatures embryos were only developed after fertilization.

Strasburger found that in *Marsilia Drummondii* the nuclei of the female gametophyte contain 32 chromosomes which is the sporophytic or diploid number present in various vegetative regions of the sporophyte. The process of sporogenesis presents various irregularities: the number of megaspore mother-cells is less than 16 and at times only 4; sometimes the mitoses within these cells are reduction divisions of the usual type (heterotypic), but in other cases spores are formed only through vegetative mitoses in which the sporophytic or diploid number of chromosomes (32) is retained. Such spores give rise to female prothallia with eggs having the sporophytic number of chromosomes and a parthenogenetic development of the latter follows. These conditions differ from those of apospory in the fact that spores are developed, but agree in the final result that the process of chromosome reduction is suppressed in the life history. The microspores showed irregularities in their development and on germination did not produce mature sperms. Two other species in the genus, *Marsillia macra* and *M. Nardu,* presented similar conditions.

Perhaps the most important feature of this cytological research on apogamy is its bearing on current theories of the nature and basis of alternation of generations in plants. It is perhaps rather generally held by those who accept the antithetic theory that the differences between sporophyte and gametophyte are in some way concerned with the number of chromo-

[3] Strasburger, E. Apogamie bei Marsilia. Flora, XCVII, p. 123, 1907.

somes, the sporophyte taking its peculiarities because of the doubling of the number which results from the sexual fusion of gamete nuclei, and giving up these characteristics when the number of chromosomes are reduced at the end of the sporophytic phase. This view that nuclear structure and more particularly the number of chromosomes gives the physical basis for alternation of generations was originally stated by Strasburger and has received support from a large amount of research on life histories throughout the plant kingdom. It has in the opinion of some authors reached the stage worthy of statement as a law of development, as indicated by the expression x and 2x generations applied to gametophytes and sporophytes.

However, the cytological investigation of apogamy in the seed plants as well as in the ferns has shown for a considerable number and wide range of forms that the gametophyte generation may have the sporophytic number of chromosomes, and now in Nephrodium there is established the first instance in which a sporophytic generation may develop with the gametophytic number.

This evidence may be regarded by some as cutting at the roots of the antithetic theory of alternation of generations, but this does not follow. It is clear that an increase or decrease in the number of chromosomes within a certain range does not affect the morphology of the phase of the plant's life history concerned, and the cause of the specific characters of gametophyte and sporophyte must rest upon other factors. What these may be is problematical; it is not unlikely that a variety of factors is concerned. It is probable that the peculiarities of every species demand at least a certain amount of chromatin with a specific composition, but there is no reason to assume that this must be contained in a fixed number of chromosomes, and furthermore multiples of the minimum amount required would not be expected to introduce new characteristics except as it might give increased vigor or vitality. Then there is the cytoplasm to be considered and perhaps of even greater importance the complex reciprocal relations that must exist between the nucleus and cytoplasm.

Bradley M. Davis.

EXPERIMENTAL EVOLUTION

Regeneration in Lumbriculus.[1]—In the August number of Roux's *Archiv* a paper by Conrad Müller describes regeneration in *Lumbriculus variegatus* and *Tubifex rivulorum.* The paper of 70 pages contains 24 figures and 14 full-page tables. Despite its bulk one can not help being impressed with its failure to contribute much that is new to our present knowledge of regeneration in Lumbriculus.

Müller's chief concern seems to be the extent of the power of regeneration. He first studied the power to regenerate a head or a tail in Lumbriculus, and from a great many experiments, very elaborately described, he found that new heads may regenerate 17–22 times in succession, while new tails regenerate 33–42 times after successive operations. From these facts he draws the general conclusion that the power of posterior regeneration is twice as great as the power of anterior regeneration. Bonnet in 1741, in his classical investigation of the regeneration in Lumbriculus, found also that heads and tails regenerate several times after successive operations—only Bonnet never obtained regeneration so many times.

These results of Müller may be, however, interpreted otherwise than that the power of posterior regeneration is greater than the power of anterior regeneration, since the worms regenerating tails had heads and could therefore feed, while the worms regenerating heads could not feed.

Regarding the relation between length of time during which a tail regenerates and the number of segments that are produced Müller sets up the following "law"—"The number of segments newly formed stands in direct relation to the length of time of regeneration; i. e., during equal periods of time there are regenerated posteriorly equal numbers of segments." He also investigated the number of posterior segments that regenerate after successive operations performed at regular intervals. In the course of ten months he cut off the regenerating tails 22 times (every 14 days) and found that in this case also "after repeated removals of a regenerating tail the same number of new segments is formed during similar periods of time." He then refers to my work on regeneration in Lumbriculus and says that, "Bei dem von Morgulis und mir behandelten Object scheint

[1] *Arch. f. Entwicklungs u. d. Organismen,* XXVI, 1908.

dass kein Unterscheid zu machen.'' But this ''agreement'' is due apparently to a misunderstanding. On the contrary, I got the opposite result in my studies on regeneration in Lumbriculus. I found that the number of segments formed within equal lengths of time decreases the more the time that has elapsed since the operation was performed. Concerning the rate of regeneration for similar periods of time (but after successive operations) my statement is so simple that it is surprising that it should have been misinterpreted. I said—'' . . . in the course of the second period of two weeks the pieces regenerate about one half as many segments as when regenerating for the first period of two weeks.'' After a third period of two weeks ''the pieces have regenerated only about one half as many segments regenerated for the second period of two weeks, and about one fourth as many as for the first two weeks.''[2]

Müller quotes my general conclusion, based upon these facts, that ''a piece of worm, when subjected to the operation of cutting a few times will produce more new tissue for the same length of time than when subjected to cutting only once,'' and says: ''Desartiges habe ich ebenfalls beobachted.''! But unless I misunderstood Müller's point, his ''law'' is the reverse of my conclusion. He says that a worm regenerates on an average 25 segments in 14 days; after the following 14 days it will have regenerated 50 segments, or 25 segments more, etc., so that the number of regenerating segments is in direct proportion to the length of time. His tables show also that when the tails have been cut off every 14 days 25 new segments regenerate each time. In other words, a worm left to regenerate for 8 weeks should regenerate 100 segments (25 segments every 2 weeks), while another worm in which the tail is removed at the end of every 14 days regenerates 25 segments after each successive operation, and, therefore, will also have formed 100 segments at the close of 8 weeks.

So that a worm that had been operated upon 4 times regenerates 100 segments in the same time in which another worm, that had been operated upon only once, also regenerates 100 segments. This certainly does not uphold my contention; it is also evident that Müller's ''law'' is incompatible with my conclusion cited above, yet he seems to find them both to be true. Müller speaks at great length of the regeneration of pieces of

[2] *Jour. Exp. Zool.*, IV, 1907, pp. 561 and 562.

Lumbriculus without adding anything new. His discovery that single segments are capable of anterior as well as posterior regeneration is not new, since I have shown in my paper, published ten months earlier, that single segments regenerate in this way. Although Müller reviews my experiments with single segments in full detail, he feels dubious as to whether I really did have single segments regenerating. The scepticism is due to the fact that, according to my description, the worms have been regenerating in clean water, and in Müller's experience "war das Halten der Tiere in reinem Wasser einfach ausgeschlossen." I may therefore mention in this place that pieces of Lumbriculus have been reared in clean water even by Bonnet, and that for the three years that I have been studying regeneration in Lumbriculus the worms were and are now *invariably* kept in clean water.

In the chapter dealing with the regeneration of regenerated pieces Müller makes no mention of my experiments, which in fact were the first experiments of that nature in Lumbriculus. He states that he got the regenerated tail, when detached from the parent body, to regenerate new heads or tails 23 times.

The fact that Lumbriculus can regenerate its head 23 times and its tail 42 times in succession is of considerable theoretical importance, and even more so is the statement that regenerated pieces are also capable of regenerating heads and tails many times in succession. It seems to me that these facts bear directly on the hypothesis of formative substances. If such substances are connected with the regeneration of a head or a tail it would be hard to conceive how such an enormous quantity of head- and tail-forming substances has become stored up in the cells to insure the possibility of regeneration after 23–42 operations, unless a further assumption is made that those substances themselves are capable of reproduction. Still harder would it be to conceive how a regenerated tail, the supposed product of tail-forming substances, has become stored up with such an abundance of reserve formative substances as to be able to produce heads or tails time after time. To make such a demand on our credulity would be asking a great deal.

Müller's work on Tubifex is practically a repetition of his work on Lumbriculus. There he finds that a head regenerates only when 4–6 anterior segments are removed, and does not regenerate more than 7 times in succession, while a tail may regen-

erate even 40 times. The successive regeneration of heads may be checked by the regeneration of the tail. Regenerated parts when detached from the worm are not capable of new regeneration.

The most novel part of the paper is that which describes various cases of heteromorphosis, and other malformations in the regenerating tail, including the regeneration of double tails in Lumbriculus or of triple tails in Tubifex.

SERGIUS MORGULIS.

September 7, 1908.

THE BUDGETT MEMORIAL VOLUME

John Samuel Budgett, naturalist, explorer, scholar and artist, was born in Bristol, England, in 1872. He received his education at University College in Bristol, and later at the University of Cambridge, where he received the appointment as Balfour Student in Natural Sciences, "the zoological blue ribbon of Cambridge." Here he gave, in 1902, a course of lectures on on the "Geographical Distribution of Animals," succeeding in this work the eminent ornithologist, Professor Alfred Newton. His work at Cambridge was interrupted and enriched by zoological exploring expeditions to South America and to Africa, efforts which from the natural history side were successful in the highest degree, but which ultimately cost him his life.

The first of these, in 1896, was to the Swamps of La Plata River at Gran Chaco in Paraguay, in search of the singular mud-fish, *Lepidosiren paradoxa.* The life history and embryology of this fish was expected to throw much light on the nature of the order of Dipnoans to which it belongs. All stages of the life history of *Lepidosiren* were represented in the collection made by Mr. Budgett, and the expedition was brilliantly successful.

On the next expedition, in 1899, he visited the Gambia River, where another genus, Protopterus, of the same group of mudfishes is found.

In the third expedition, in 1900, he visited the Gambia again, gathering material for not only the life history of the dipnoan, Protopterus, but of different species of the equally interesting

[1] The work of John Samuel Budgett, Balfour Student at the University of Cambridge, edited by J. Graham Kerr, University Press, Cambridge, G. P. Putnam Sons, New York, p. 422 quarto, with many engravings in stone. Price $7.00.

crossopterygian, Polypterus as well. With this was obtained material for the study of Gymnarchus and other peculiar fishes of the African streams.

In 1902, Mr. Budgett undertook an expedition to Nyanza and the head streams of the Nile.

A final trip was made in 1903, to the Niger River, in which, as in the others, he found species of Polypterus, and with which he made most interesting experiments in artificial fertilization.

In all of these expeditions, Mr. Budget found what he sought, and their importance to science can hardly be too highly estimated. The embryology, taxonomy and geographical distribution of these fishes, as well as of different genera of frogs, received notable accessions. But Mr. Budgett's health was sacrificed in the work. A recurrent attack of "blackwater fever," one of the many diseases known as malaria, caused his death on January 19, 1903, at the age of thirty-one.

The publications of Mr. Budgett give the record of these expeditions, and also discussions of the anatomy, the embryology and the breeding habits of Polyterus, Protopterus and other species. The batrachians of the Paraguayan Chaco are described in detail, and there is a paper on the birds of the Gambia River.

All these papers of Budgett, with others by Dr. G. A. Boulenger, Dr. J. Graham Kerr, J. Herbert Budgett, Richard Assheton, Edward J. Bles and Edward T. Browne, based on material collected by Mr. Budgett, have been sumptuously printed in the present memorial volume by Mr. Budgett's friends and fellow-workers at Cambridge. A delicately appreciative biographical sketch of Mr. Budgett is contributed by Dr. Arthur E. Shipley. In this are extracts from Mr. Budgett's diaries, showing his fine appreciation of nature and his charming and forceful use of English. The plates illustrating this volume are worthy of the text, and the whole is a noble memorial to an able naturalist, a brave and lovable man, who fell untimely from the hazards of his chosen calling.

David Starr Jordan.

ANIMAL BEHAVIOR

Mind in Animals.—Many experimentalists have said in their haste that all comparative psychologists are liars; that comparative psychology has no existence. To the experimental student of animal behavior, working by the methods of physiology and zoology, "psychic factors" are merely an irritating *x*, something which he can not perceive in his work, yet which the philistine is continually trying to force upon him as the cause of what he does perceive. Finding objective determining factors for all the objective phenomena, he has no use for the psychic factors, and finally decides to make war upon the whole worthless mess; Down with comparative psychology! is his cry.

But it is really only as a technician, intent on the proper methods for his own work, that the experimentalist can object to comparative psychology. As soon as he takes a wider view, he must perceive that another group of men have made a life specialty of precisely the matters that he leaves out of account, and he can not expect these men to give up their interest in the distribution and development of the phenomena that they are studying—of mind and mental processes. And so we have here two recent scientific works dealing with the presence of mind in animals, both from the experimental standpoint, one by a psychologist,[1] the other by a zoologist.[2]

Miss Washburn's book is of the greatest interest and value, supplying a need much felt. It will be the standard work for those who wish to know the present position of scientific animal psychology. Concerning the behavior of animals a large body of verifiable facts, which have begun to shape themselves into a more or less intelligible system, has been gathered together by experimentalists, but the latter have given little but hostile attention to the psychic aspects of the matter. What are the implications of this body of facts concerning the distribution of psychic processes among animals? This is the problem which Miss Washburn sets herself—a problem in which doubtless full as many are interested as in behavior as a purely objective

[1] Washburn, Margaret F. The Animal Mind: A Text-book of Comparative Psychology. New York, The Macmillan Co., 1908. $1.60. (Volume 2 of the Animal Behavior Series, edited by R. M. Yerkes.)

[2] Strassen, Otto Zur. Die neuere Tierpsychologie. Vortrag in der zweiten allgemeinen Sitzung der 79. Versammlung deutscher Naturforscher und Aerzte zu Dresden (1907). Leipzig und Berlin, B. G. Teubner, 1908.

science. One need not hold that psychic factors are required for explanation of the objective facts in order to see the great interest of this inquiry.

The author therefore examines systematically the behavior of animals, as discovered by experiment, from Amœba to the apes, attempting to show what psychic processes are, or may be, implied. She readily admits the possibility that no psychic processes are present at all; but the question is this: If we assume that psychic processes *are* present, and that they follow rules like those which they follow in man, then what ones appear to be present in the different groups of animals? In answering this question, the principle of parsimony is taken as a guide: "in no case may we interpret an action as the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale." The undeniable dangers of this, in the evident fact that nature doesn't always operate by what seems to our limited view the simplest means, is expressly recognized, but the principle is thought valuable for holding in check the common tendency to attribute higher intellectual faculties to animals—a tendency, we may remark, which in very recent times shows some inclination to change into its opposite.

After judicious introductory chapters on Difficulties and Methods; on the Evidences of Mind, and on Mind in the Simplest Animals, the main divisions of the book are devoted to Sensory Discrimination; Spatially Determined Reactions; Modification by Experience; the Memory Idea, and Attention. The devotee of popular animal psychology will be surprised to find that the word *reason* does not even occur in the index. The facts of behavior are set forth clearly and accurately; the student even of the strictly objective aspects of the subject will find this perhaps the best compendium of the important facts that exists. The treatment is throughout sane and conservative; it is analytic, systematic and scientific—not in any sense popular, though clear. Slips as to facts and details appear to be rare. All together the treatment appears to one not a psychologist—to one who "wants to be shown"—most satisfactory. Such a discussion of these matters by a competent psychologist has been much needed.

The book gives the experimentalist an opportunity to compare as to solidity and general satisfactoriness, his own objective

science, built up by systematizing the verifiable facts alone, with that which searches for the psychic processes underneath what is observed. The difficulties of making a positive science from the unverifiable psychic implications of the actions of animals is well illustrated by the conditional and potential forms in which the author is forced throughout to clothe her statements. Thus, in discussing the psychic aspect of orientation to light (p. 184), the predicates of six successive sentences are: we "cannot imagine"; we "may conjecture"; "is the human experience most closely resembling"; "appears to be"; "may have"; it "is possible that." The experimentalist becomes convinced more than ever of the need of building up his own positive science of behavior, composed of verifiable propositions, and omitting psychic factors—though there is no reason why he should look with an unfriendly eye on the attempt, as a separate thing, to supply conjecturally the missing psychic elements.

The difficulties in preparing a satisfactory account of the animal mind are further increased by the high degree in which the experimental science of behavior shares the provisional and uncompleted character of all science. Animal behavior even as a purely objective science is merely in its beginning. No greater mistake could be made (and this our author evidently recognizes) than to suppose that our present experimental knowledge is sufficient for defining sharply the psychic powers of animals. It is quite possible that the picture of the mind of one of the higher animals that might be drawn by an observing and judicious dog lover would be much more adequate than the rude sketch which experimental science is now able to give us. The material furnished by the old Anecdotal School, and by the Lovers of Nature, doubtless contains much most-important truth, to which the experimental method has not yet succeeded in attaining: only, as Miss Washburn says, it is not possible to tell what *is* true, what false. This material furnishes valuable finger posts for experimental investigation, but if we are ever to be able to distinguish the true from the false in animal behavior, it is necessary to build up the science by that slow and painful addition of one verifiable fact to another, which has proved the method of advance for other sciences. At any given time then our experimental science and the psychology based upon it are bound to be incomplete and inadequate to the reality. A single illustration must suffice. Miss Washburn shows that a careful

analysis of the experimental facts indicate that in Crustacea there is no color vision. But in the short period since her account was written, Minkiewicz has demonstrated experimentally a refined color vision in this group, the animals standing with much success the test of "matching colors" for their disguises. If in so comparatively simple a matter the negative indications were wrong, how much dependence can be placed on our now having a complete knowledge of what exists in higher spheres? Every experimenter knows how near he came to missing some important result that he finally reached; he realizes that there are doubtless many things equally important that he *did* miss. The positive results of experimental science are stones for building; the negative ones are often merely space as yet unfilled. Yet such summaries as Miss Washburn gives us of the knowledge at any particular time are necessary and valuable, especially when, as in the present case, they are put together by one fully conscious of the limitations of the subject.

Zur Strassen[3] in his lecture before the German Congress of Naturalists and Physicians deals with another aspect of mind in animals; with a question of the greatest practical interest to experimentalists, and of great theoretical interest to all. Are "psychic factors" required for explaining the behavior of animals, or can we explain the behavior throughout from the experimentally perceivable, objective, factors; can animals be understood as physico-chemical machines? Zur Strassen follows a course of reasoning which is often begun, but which usually stops in the middle; the author carries it to the end, with illuminating results.

As his guide he takes the principle of parsimony in its widest sense—that we shall not assume the existence of any factor which is not required in order to explain the results. A further principle, acted upon but not set forth in words, is that mere increase of complication, no matter how great, does not in itself imply a new principle of action. Under these principles he examines a series of examples of animal behavior in successive stages of complications, from Amœba to apes, concluding in each case that the entire behavior can be understood from the standpoint of physico-chemical causality, and that therefore we are not entitled to assume the presence of any psychic factor in the matter. The author is not inclined to add or subtract from

[3] *Loc. cit.*

the facts in order to maintain his thesis; he recognizes fully the complication of the behavior of both higher and lower animals; and he does not claim that we now know the precise physico-chemical factors involved in all behavior. But he is able to make a good case for his view that all is fundamentally intelligible physico-chemically; in other words, that we could ultimately make a complete and systematic explanation of what animals do, even if we assumed that they have no "psychic factors," no consciousness, at all. The nature of the objective explanations which to the author seem satisfactory he can of course merely sketch; there is no attempt to give details or claim finality. Most significant appears to him, as to others who have studied the matter, the making by animals of varied movements, which bring them into varied relations with the environment, until certain of these relations prove advantageous and therefore persist. To this way of acting, which has received various names, including (from the present reviewer) the unfortunately misunderstandable one of "method of trial and error," Zur Strassen gives the expressive name of the "shot-gun method." Some such evidently figurative term is doubtless its best appellation, as reducing the temptation to read higher things into it.

But now we come to the case of man; do our principles of interpretation exclude psychic factors here also? Most undoubtedly they do, if the reasoning up to this point has been well based. Greater complication there is, but no difference in principle; Zur Strassen sets forth that there is no reasonable ground for making a distinction between the behavior of man and that of animals in this matter. And so, are we led to the absurd conclusion that there are no psychic processes, no consciousness, in man?

Here we perceive that two questions must be distinguished—two questions which we shall try to formulate even more sharply than the author has done, because the usual failure to distinguish them has tremendously confused this whole matter. The questions are: (1) Does mind exist in men and animals? (2) Does mind play such a part in the behavior of men and animals that a complete objective explanation of the behavior can not be given without taking it into consideration?

To this second question Zur Strassen answers, No: a satisfactory explanation of the behavior of man and animals can be given without taking into consideration any factors but objective,

physico-chemical ones. But this has no bearing on the answer to the *first* question: it is no argument against the *existence* of mind in either man or animals, for it does exist in man. It may therefore exist in animals: the author concludes, as he is bound to, that the probability is that men and animals are alike in this matter; that animals also are conscious. His only contention is that mind is not a *factor* in determining objective behavior; or as the reviewer would prefer to put it, that a complete objective explanation of behavior can be given without taking into consideration consciousness.

Zur Strassen's discussion brings out two points that much need recognition. (1) If we adopt the principle of parsimony of explanation as a test for the *existence* of psychic qualities, as has been done by various authors, we inevitably come to the result that such qualities do not exist, even in places where we know, by direct experience, that they do exist. When I withdraw my burned finger from the flame, consciousness is no more required for an objective explanation of this action than it is for the withdrawal of Amœba under similar conditions, yet in my case there *is* consciousness, of a very intense character. Therefore the result of the application of this principle of parsimony is no test whatever for the existence of psychic qualities. A consistent carrying through of the principle places man and animals in the same category, and is therefore, as Zur Strassen maintains, rather favorable than otherwise, to the general distribution of consciousness in animals.

(2) Admission of the existence of consciousness in animals is not equivalent to holding that consideration of this consciousness is required for a complete objective explanation of behavior. This point needs to be sharply realized. Look at the matter experimentally. A complete explanation, from an experimental point of view, is one in which the preceding condition is shown to contain differential factors for determining all the differentiations of the succeeding condition. The question whether consciousness is a "factor" requiring consideration in objective explanations resolves itself experimentally into this: Do we sometimes, in analytical experimentation, come to situations where there are no differences in experimentally perceivable factors to account for differences in our results? If we could perceive accurately all the objective factors present, should we find that sometimes two identical combinations give different

results? If so we might be compelled to conclude that some factor *x*, not perceivable objectively—a psychic factor, perhaps—is playing a part. And this of course would mean the bankruptcy of the experimental method; it would mean that things happen which are not determined, so far as experiment can show; that when differing results appear in two cases, we cannot look with confidence for any antecedent differences in the conditions to explain them; that by supplying the same conditions in two cases we can not be sure of getting the same results; it would mean that nature plays fast and loose with us so far as objective experimentation is concerned. To the experimentalist the question whether states of consciousness may at times come in and alter his results, without the accompaniment of changed objective conditions to which the changed results can be attributed, is evidently an intensely practical one, and so long as this possibility is held open, it is idle to tell the experimenter that he should not concern himself about psychic processes.

But if, as is commonly held, states of consciousness are always accompanied by objective physiological conditions, and these objective conditions differ when the conscious states differ, then of course we should always be able to find satisfactory objective determining factors for all differing results; a complete experimental explanation of what happens could be given, without taking into consideration unknown states of consciousness; the objective experimental method would be reliable. There seems to be no convincing evidence as yet that it is not reliable and sufficient unto itself; it will be best to hold to it till such evidence appears. And yet, as we have seen, to hold to it as reliable and sufficient does not imply in the least that states of consciousness do not likewise exist.[1] Comparative psychology and a purely objective science of animal behavior, complete in itself, may exist side by side without the least conflict.

H. S. JENNINGS.

[1] It does not even imply, I believe, that consciousness is without effect on action. A good case could be made for the effectiveness of consciousness, in a widened experimental sense, even though a purely objective explanation, without gaps, can be given for behavior.

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SOME PHYSIOLOGICAL EFFECTS OF RADIUM RAYS[1]

PROFESSOR CHARLES STUART GAGER

NEW YORK BOTANICAL GARDEN

IT is probable that no scientific discovery, since the publication of Darwin's "Origin," has so revolutionized our conceptions of natural phenomena as has the discovery of radioactivity by Henri Becquerel, and of radium, by M. and Mme. Curie and Bémont. In the light of these epoch-making discoveries we have completely revised our concepts of the nature of matter and of electricity. The atom, the "undivided," has been shattered into fragments, and a large percentage of the investigations in the realm of physics and chemistry now have to do with atomic disintegration and the behavior of the resulting products.

It was Rutherford and Soddy who first proposed the hypothesis that radioactivity is a manifestation of the disintegration of atoms, and this hypothesis, chiefly through the investigations of Rutherford, has already assumed the rank of a theory.

It would be superfluous to enter here into a detailed account of the nature of radioactivity, as understood at present. Suffice it to say that the theory elaborated by

[1] The investigations embodied in this paper are treated more fully in the author's memoir on "Effects of the Rays of Radium on Plants" (*Mem. N. Y. Bot. Garden,* **4**. Sept., 1908). It has not been thought desirable to enter into a discussion here of previous researches on the subject, since the literature is fully treated in the memoir. It is a pleasure again to express my indebtedness to Mr. Hugo Lieber, of Lieber & Co., New York City, whose great liberality in supplying all the radium made the investigation possible.

Rutherford involves a conception of the atom as a body composed of intricately related units. These units possess relatively enormous amounts of kinetic energy, and are in rapid orbital motion within the atom. In some substances of high atomic weight, such as uranium, polonium and radium, these units spontaneously escape from the atom and fly off into space. Such substances are called radioactive, and the emission of these units is radioactivity.

The particles themselves are called ions. They are of at least two kinds; one, called the β particles, very small (about one one-thousandth the size of a hydrogen atom), bearing a charge of negative electricity, and moving with a velocity approaching that of light; the other called α particles, about twice the size of a hydrogen atom, bearing a positive electrical charge, and moving at a much lower velocity than the β particles. The β particles or negative ions are called electrons.

Streams of negative electrons constitute the so-called β rays; streams of positive ions the α rays. Both α and β particles move with velocities that vary between certain limits and so the respective rays are complex.

In addition to the giving off of α and β rays, radioactivity involves the emission of electro-magnetic pulses in the ether. These are analogous to very penetrating X rays, and are called γ rays.[2]

The enormous velocity of the β particles, combined with their inconceivably small size, renders them very penetrating. They pass readily through matter opaque to light, moving between the molecules, or even passing directly through the latter, being smaller than the spaces by which the atoms are separated within the molecule. In their passage through substances they may collide with and so dislodge other electrons, thus producing ionization. The α particles, owing to their larger size

[2] Jean Becquerel (*Compt. Rend. Acad. Sci. Paris*, **146**: 1308. 22 Je 1908, **147**: 121. 13 Jl, 1908) reports the experimental demonstration of the existence of free *positive* electrons, but whether such electrons are involved in radioactivity has not been determined.

and lower velocity, are less penetrating than the β particles, but are much more effective ionizers. The γ rays behave as X rays.

In addition to the three types of rays above described, radioactive substances are the source of a heavy, inert gas, belonging to the argon family. This gas, named by Rutherford the emanation,[3] is itself radioactive, giving off only α rays.

Studies of the physiological effects of radium, therefore, must take into consideration the three types of rays, described above, and also the radioactive gas, the emanation. In the experiments recorded below, the radium, in the form of radium bromide, was contained in sealed glass tubes, or employed as a thin coating on a suitable surface. In the former case only X and γ rays were available, as the α rays and the emanation can not pass through the walls of the tubes. In the latter case the α rays together with the emanation were also available.

The effects of radium upon plants have been investigated by Dixon and Wigham[4] in Great Britain, by Koernicke[5] in Germany, by Guilleminot[6] in France, and by several others. Without going into the details of their work it may be stated that the general conclusion from their experiments is that the rays exert either a retarding or an inhibiting effect on physiological processes. Koernicke, however, found some evidence that acceleration of activity might follow exposure to the rays under suitable conditions.

My own investigations have led to the conviction, already reported,[7] that radium rays act as a stimulus to

[3] The use of the plural "emanations" to designate all the rays and influences coming from radium, has been somewhat common in biological papers. It has no warrant, is only confusing, and should be abandoned.

[4] *Nature,* **69**: 81. 1903. *Proc. Roy. Dublin Soc. Sci.,* N. S., **10**^{2}: 178. 1904. *Notes Bot. School, Trinity Coll.,* Dublin, **1**: 225. 1905.

[5] *Ber. Deut. Bot. Ges.,* **22**: 148, 155. 1904; **23**: 324, 404. 1905.

[6] *Compt. Rend. Acad. Sci. Paris,* **145**: 711. 1907; *Compt. Rend. Assoc. Française Adv. Sci.,* **36**^{1}: 389. 1907; **36**^{2}: 1344. 1908; *Compt. Rend. Acad. Sci. Paris,* **145**: 798. 1907.

[7] "Effects of the Rays of Radium on Plants." New York, 1908. (*Mem. N. Y. Bot. Garden,* Vol. IV.)

plants. If this stimulus ranges between a minimum and an optimum point an excitation of function results; if beyond the optimum point a depression of function, passing to complete inhibition as the strength or duration of the treatment is increased beyond the point of optimum stimulation. The following experiments are chosen from nearly 200, and indicate the nature of the evidence upon which the above conclusions are based.

Eight dry seeds of the bean (Phaseolus—Henderson's "Long Yellow, Six Weeks") were placed in moist sphagnum with their hilum-edges touching a rod coated with a Lieber's radium-coating[8] of 10,000 activity.[9] After

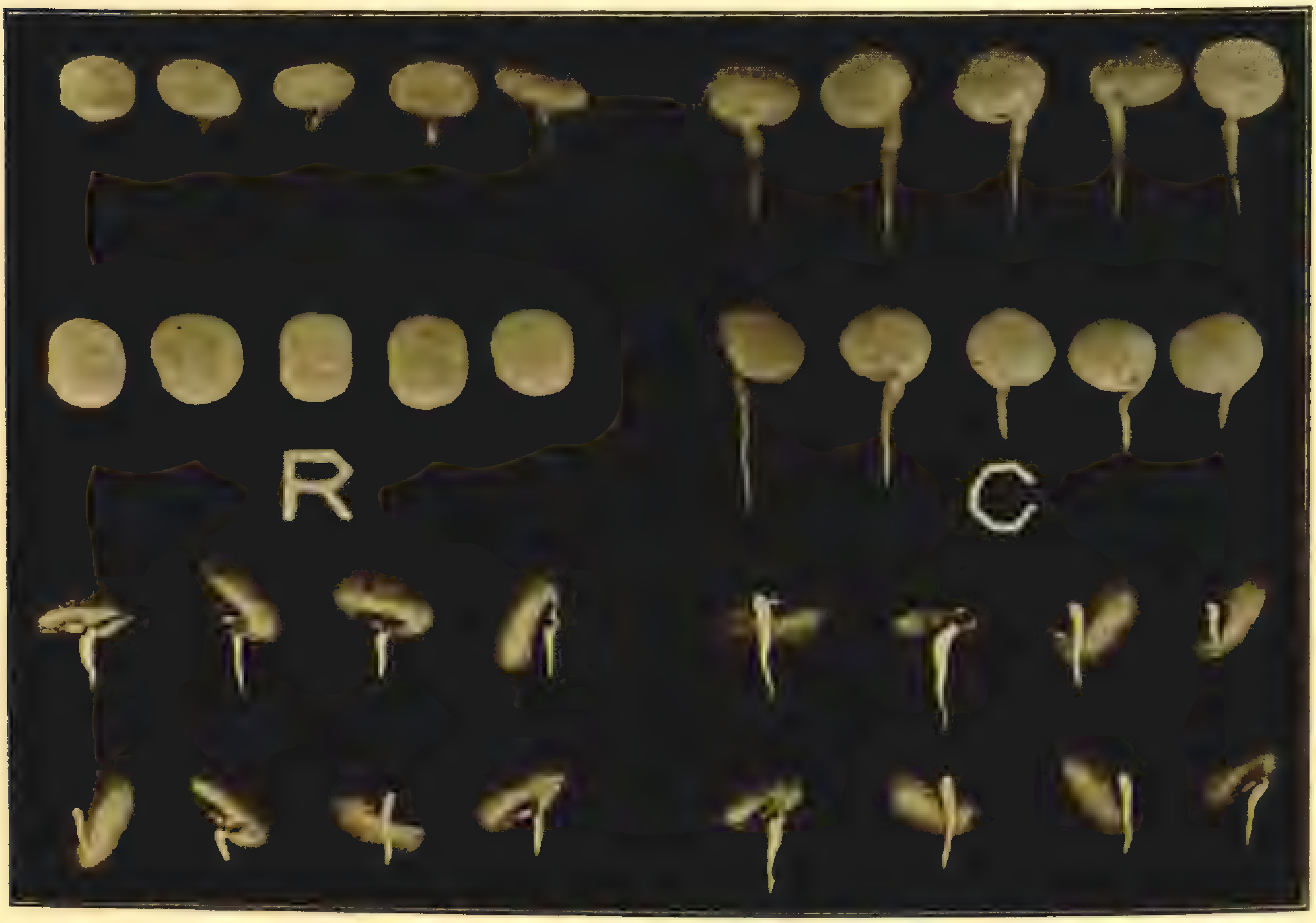

Fig. 1. Effect of radium rays on the germination of *Lupinus albus* and *Phaseolus*.

three days (70 hours) exposure, the radicles of the exposed seeds averaged 13.18 mm. in length, those of a control set 15.12 mm. Ten dry seeds of *Lupinus albus* were similarly exposed to a coated rod of 25,000 activity and,

[8] See Gager, *l. c.*, Chapt. VI.

[9] The unit of activity is the activity of uranium. Radium of, *e. g.*, 10,000 activity is 10,000 times as active as uranium.

at the end of three days (70 hours) the radicles of the exposed seeds averaged 3.81 mm. in length, those of the control set 21.80 mm. The retardation of germination and growth following this treatment is illustrated in Fig. 1.

A row of timothy grass seed (*Phleum pratense*) was sown on a moist blotter. Over the center of the row was suspended vertically a sealed glass tube containing 10 mg. of radium of 1,500,000 activity in the end of the tube nearest the seeds. The distance from the tube to the seeds was about 5 mm. A second row was also arranged as a control (not exposed to radium). At the end of eleven days the control seedlings were all of about the same height and color (normally green) and averaged 30 mm. in height. The exposed plants were entirely etiolated directly under the radium tube and for a radius of 4 mm. on each side. The height of the seedlings gradually decreased from 30 mm. (average) at the

FIG. 2. Effect of radium rays on the germination and growth of timothy grass.

ends of the row, to 3 mm. at the center under the radium (Fig. 2).

Twenty seeds of "Lincoln" oats (Avena), with the glumes removed, were placed in two parallel rows with the radicle ends touching, and the embryo-side uppermost. Over them was laid the sealed glass tube of radium bromide of 1,500,000 activity, resting on the radicle ends of the seeds. After an exposure of 6 days

and 15 hours, these grains, together with twenty similar but unexposed ones, were planted in flower pots in soil. The control grains germinated two days sooner than those exposed, and, at the end of seven days after planting, the seedlings from the exposed grains were just appearing above the soil, while the control plants were several centimeters tall (Fig. 3).

FIG. 3. Effect on the germination and growth of oats of exposing the grains before planting. Cf. Fig. 4.

In order to test the effect on germination and growth of radium rays in the soil, 16 unsoaked grains of "Lincoln" oats were sown in soil in a flower pot, in 3 concentric circles, at distances of 7 mm., 22 mm. and 45 mm. from the center of the pot. At the center

FIG. 4. Acceleration of germination and growth of oats by placing a sealed glass tube of radium in the soil (R). The tube in C is empty. Cf. Figs. 3 and 5.

the sealed glass tube of radium (1,500,000 ×) was inserted vertically into the soil, with the end containing the radium at a depth of about 5 mm. below the surface. A control culture was similarly arranged with an *empty* glass tube. After an exposure of 106 hours the seedlings in the pot containing the radium were all up, and were most decidedly taller than those in the control culture, three of which were not yet up, and all of which were less developed in every way than those exposed to the radium.

The plants in the outer circle of the exposed culture averaged 50 mm., those in the middle circle 46 mm. and those in the inner circle 42 mm. taller than those in the corresponding circles of the control (Fig. 4).

On the sixth day after planting the radium tube was changed to the control culture, and the empty tube replaced the radium. The pot C was then irradiated (CR)

FIG. 5. The same cultures as those shown in Fig. 4, six days later. The radium tube is now in C (CR), and R serves as the control. Cf. Fig. 4.

and R became the control. At the end of five days after this change the plants in CR (Fig. 5) were nearly as tall as those in C and the exposure was photographed. Eventually the plants in CR exceeded those in R, and thus, by changing the radium tube from one pot to the other, the growth of either culture could be accelerated at will.

In order to ascertain the effect on growth of exposing seeds for the same length of time to radium of various degrees of activity, three sets, A, B and C of six dry seeds each of *Lupinus albus* were exposed to rays from radium in sealed glass tubes by laying the tubes against the hilum-edges of the seeds. The duration of exposure was 91.5 hours, and the strengths of the radium as follows: A, 1,800,000 ×; B, 1,500,000 ×; C, 10,000 ×; D, control, not exposed. At the close of the period of exposure the seeds were planted in soil, each set in a different pot. The experiment was photographed eleven days after the seeds were planted (Fig. 6), and curves of growth of the

FIG. 6. Effect on growth of exposing seeds of *Lupinus albus* for 91.5 hours to rays from radium of various degrees of activity. From left to right the activity was 1,800,000; 1,500,000; 10,000; C, control. Cf. Fig. 7.

four cultures are shown in Fig. 7. It is seen at a glance that the effect of the rays on growth varies directly with the degree of activity of the radium. The apparently anomalous rise of the 1,800,000 curve during the first days record (Fig. 7) is due either to poor exposure of some one of the seeds of that culture, or represents an individual variation in resistance to the rays that was not compensated for because of the small number of seeds necessarily employed.[10]

To show the effect of duration of exposure to radium of the same activity, four sets of six dry seeds each of *L. albus* were taken. Three of them A, B and C, were exposed as follows to the rays from 10 mg. of radium

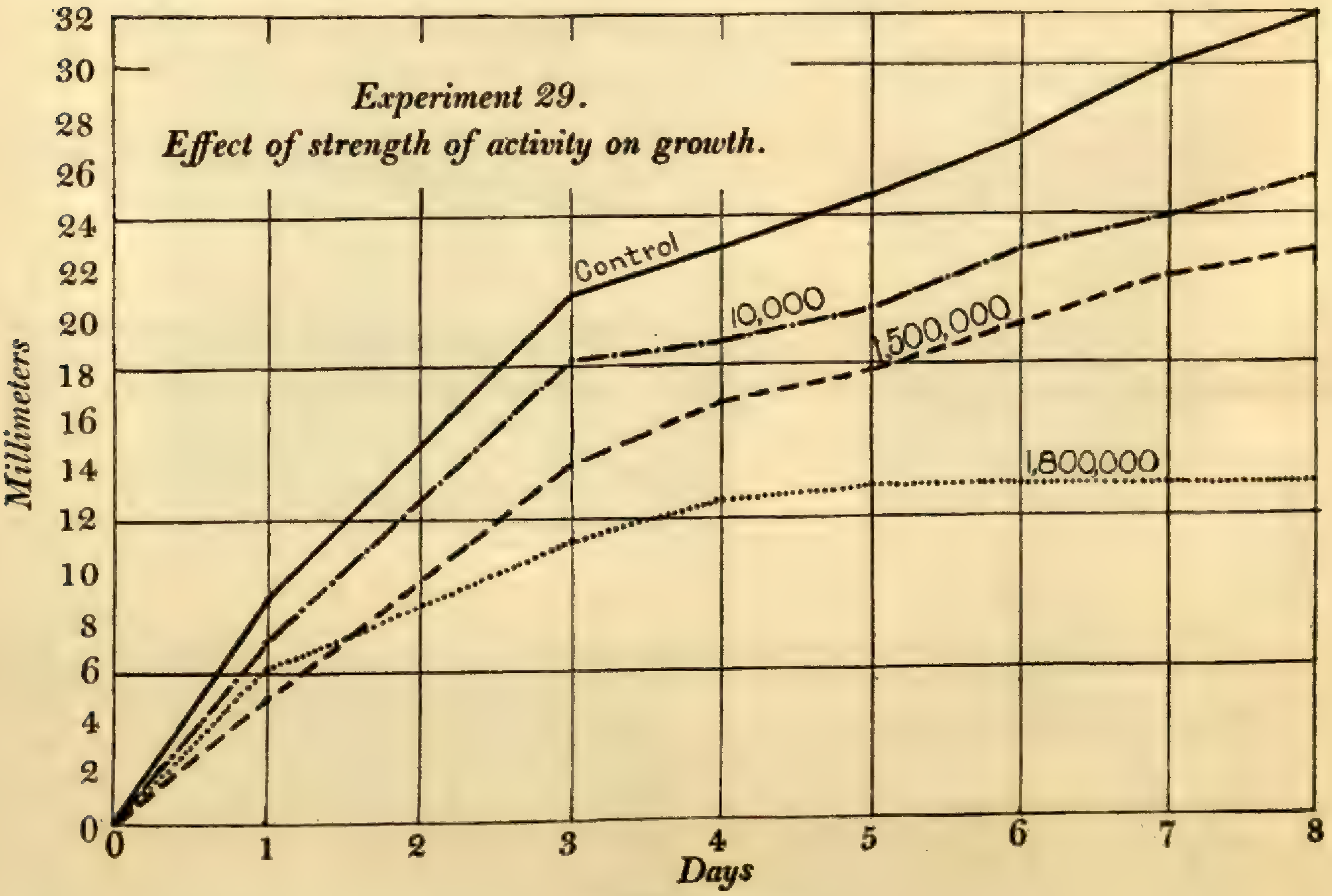

FIG. 7.

bromide of 1,800,000 activity, in a sealed glass tube: A, 72 hrs.; B, 50 hrs.; C, 26 hrs.; D, control, not exposed. The seeds were then planted, without soaking, in separate pots of soil. At the end of 5 days the average heights of the seedlings above the surface of the soil were as follows: A, 88 mm.; B, 95 mm.; C, 134.50 mm.; D, 145 mm. Inspection of the curves of growth for the four cultures (Fig. 8) shows that, for a given activity of radium, the effect on growth varies directly with the duration of the exposure.

The retardation of starch formation by a green leaf in the light was shown as follows. A nasturtium (*Tropæolum*) plant was removed to the light after being in darkness for 18 hours. Under one of the leaves,

[10] The length of the tube did not permit of satisfactorily exposing a larger number of seeds at one time.

empty of starch, was placed a Lieber's radium-coated rod of about 25,000 activity. The rod was placed under the leaf in order not to shade the latter. After an exposure of twenty-four hours the leaf was decolorized and tested with iodine. Abundant starch was found on the edge of the leaf farthest from the rod, but only very slight

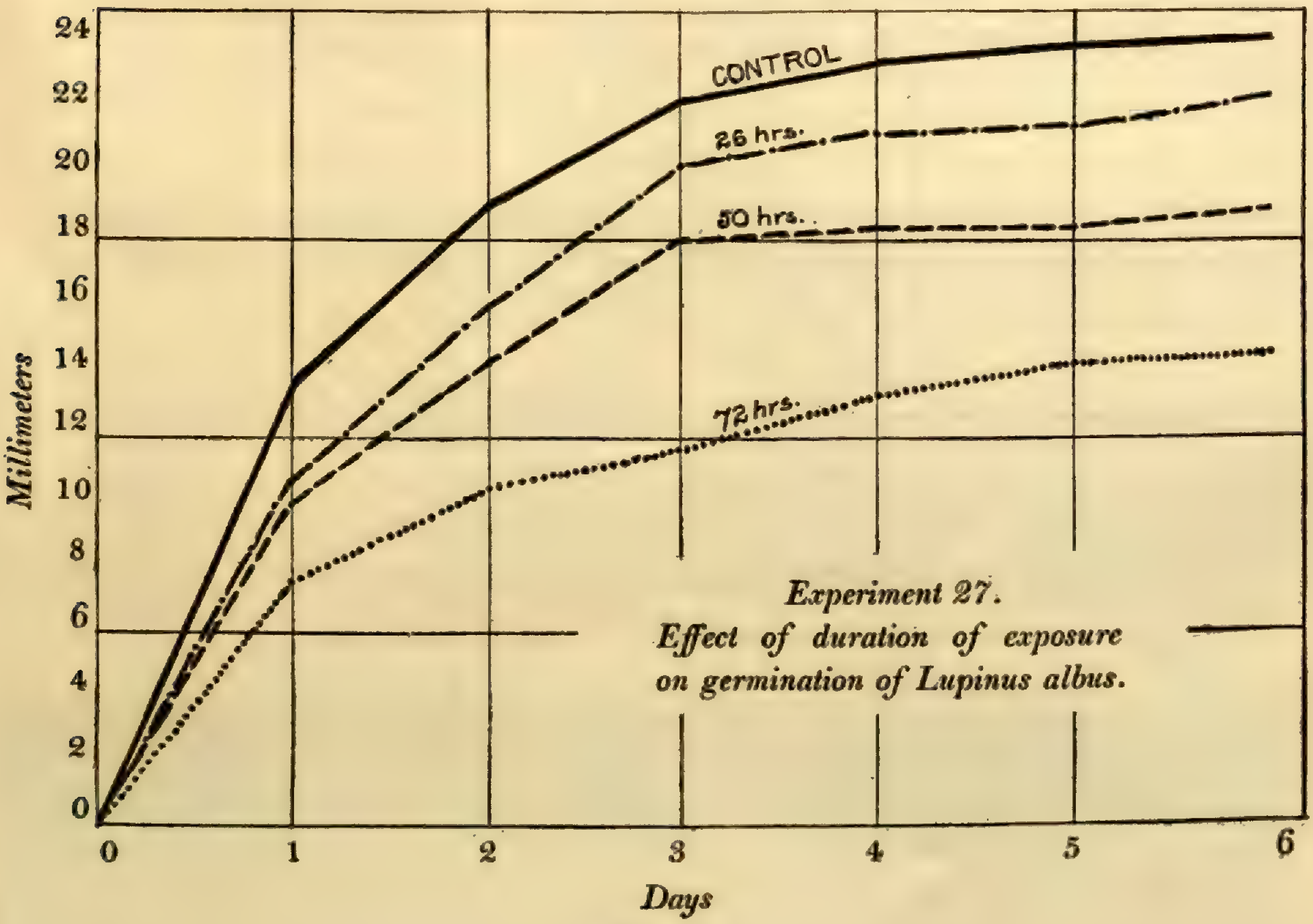

FIG. 8.

traces elsewhere, especially in the region that was directly over the rod. A print of the leaf was made by laying it over a sheet of velox paper in a printing frame and exposing it to light. In this way the portions having less starch, and, therefore, more transparent, showed darkest on the print (Fig. 9).

All attempts to demonstrate a direct tropistic response to the rays, by either roots or shoots, were unsuccessful. When, however, a sealed glass tube containing about 50 mg. of radium bromide of 10,000 activity was suspended horizontally in a culture solution, at a distance of from 2–10 mm. from the root-tips of *L. albus,* the roots curved toward the tube (Fig. 10). In an experiment in which

a culture solution was substituted for the tap-water, the angle of curvature was more abrupt (nearly 90°). It seems probable that this is an indirect response, due to the effect of the radium rays on the water or solution.

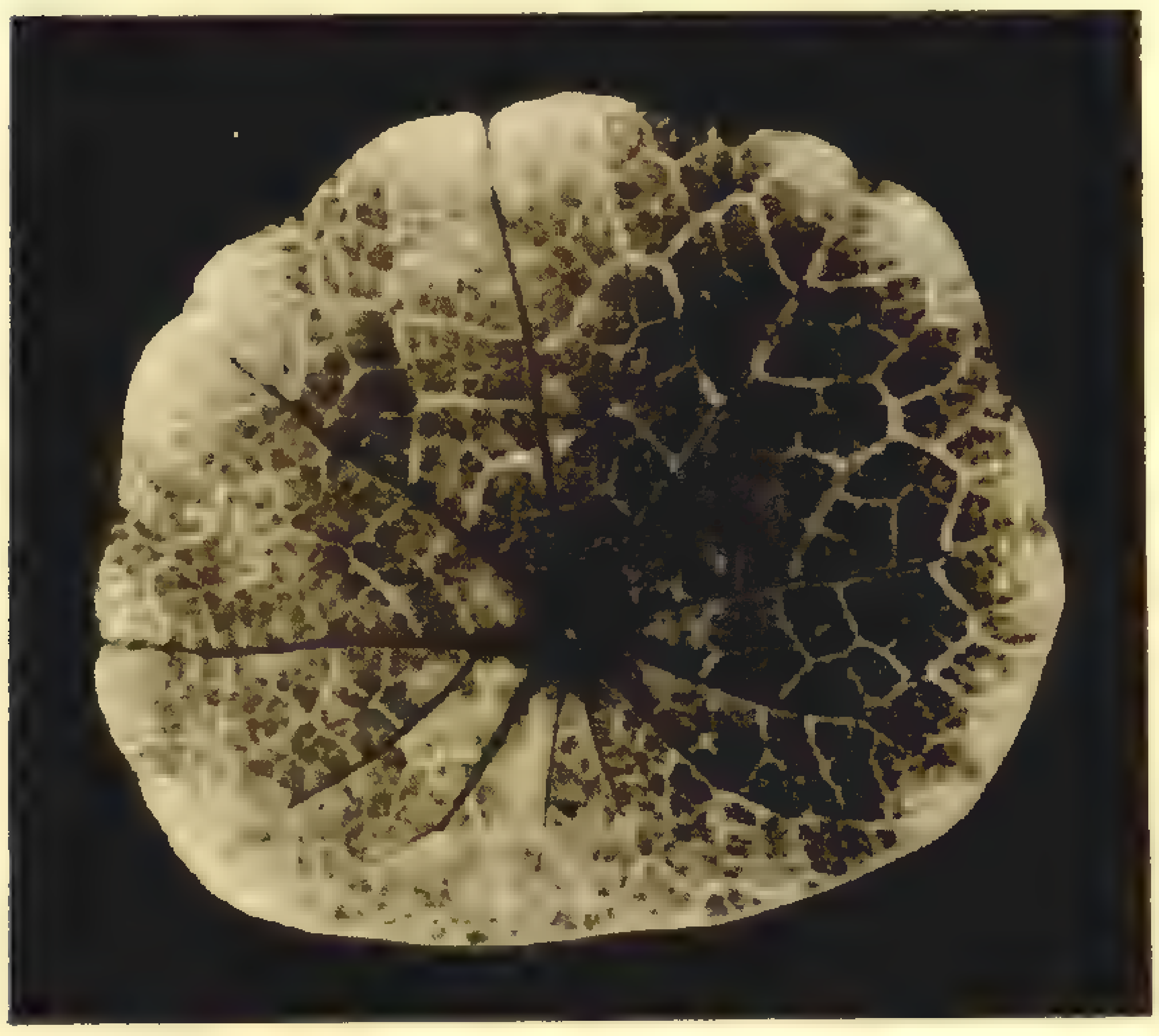

FIG. 9. Retardation of photosynthesis by radium rays. A direct heliograph, made by interposing the leaf between velox paper and the light. The darker portion represents the region exposed to the rays.

FIG. 10. Curvature of root-tips toward a sealed glass tube of radium bromide (10,000 ×) in a culture solution.

Whether the rays increase the number of ions of an electrolyte in solution is still a debated question,[11] but the physiological effects of tap-water exposed to the rays seem to leave no doubt but that the latter alter a solution in some way. How, we do not know.

Micheels and de Heen[12] were among the first to study the effect of the rays on plant respiration. Under the conditions of their experiments respiration was always retarded. In one of my own experiments, soaked grains of wheat (*Triticum*) weighing, when dry, 2 gm., were supported on a moist blotter in a tumbler over a saturated solution of KOH. Over the wheat, and in contact with the grains, was placed the sealed glass tube of radium of 1,500,000 activity. The CO_2 given off by the wheat was absorbed by the KOH, and the consequent rise of mercury in a graduated tube of small bore was taken as an index

[11] Cf. *Mem. N. Y. Bot. Garden*, **4**: Chapt. XIX. 1908.

[12] *Bull. Acad. Roy. de Belgique Class. Sci.*, p. 29. 1905. *Bot. Cent.*, **98**: 646. 1905.

of the rate of respiration. Under such conditions, and with radium of 10,000 as well as 1,500,000 activity, the result was always an acceleration of respiration, as is shown in Fig. 11. It is probable that, under certain con-

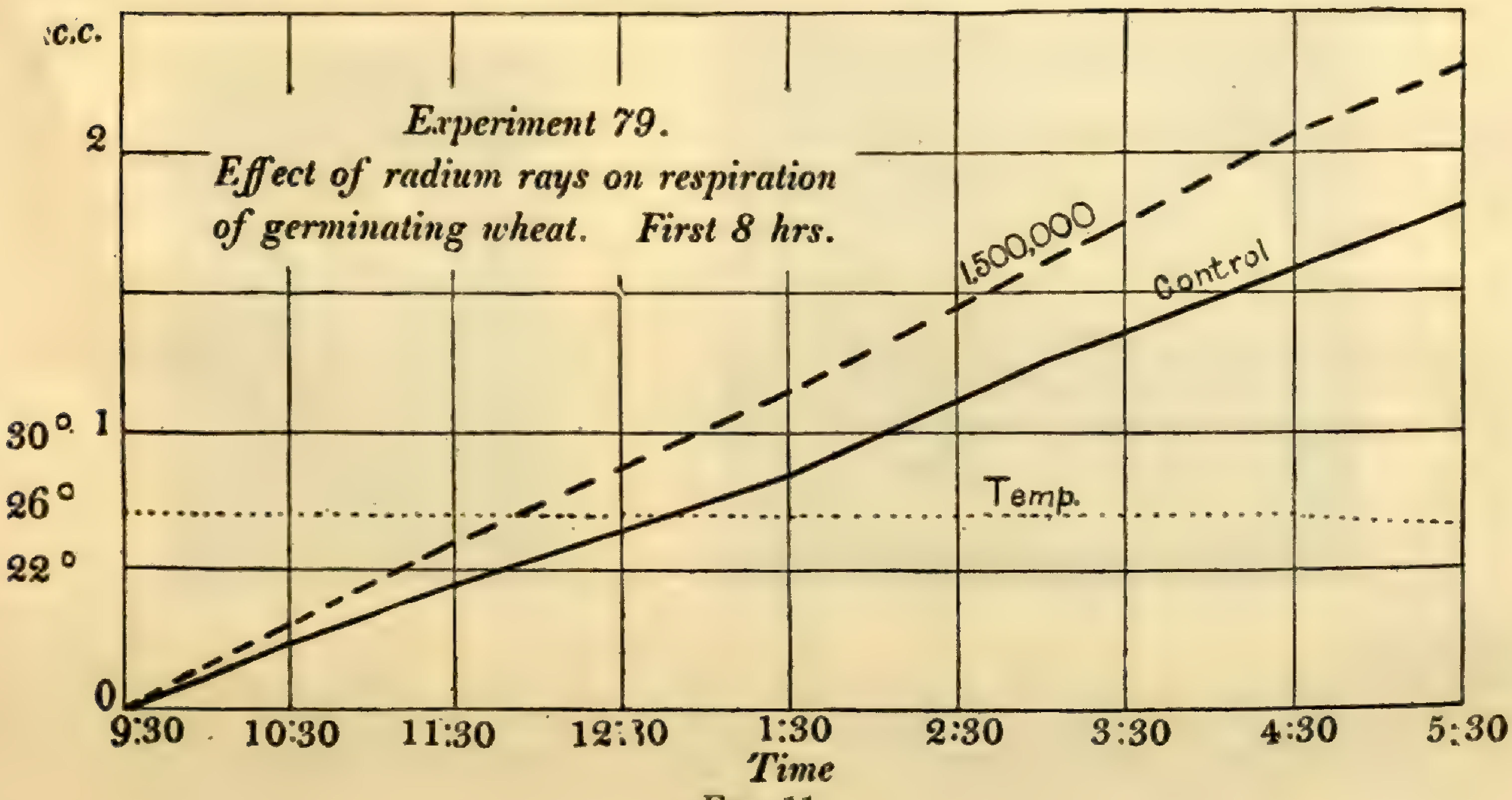

Fig. 11.

ditions of exposure, the rays would retard or completely inhibit respiration.

In order to test the influence of the rays on alcoholic fermentation, mixtures of commercial yeast in feremantation tubes were exposed to the rays. A piece of compressed yeast weighing 1 gm. was thoroughly mixed in 100 c.c. of tap-water, and equal portions of this mixture were placed in fermentation tubes. Into these tubes were placed sealed glass tubes containing radium bromide of activities 7,000, 10,000 and 1,500,000. A fourth fermentation tube with no radium served as a control. The rate of fermentation was measured by the rate of evolution of the gas. The results of all experiments indicated a decided acceleration of fermentation under the influence of the rays, and, as the curves in Fig. 12 clearly show, the amount of acceleration is in direct proportion to the activity of the radium.

No reference has yet been made of the fact that radioactivity is a factor in the normal environment of plants.

I have elsewhere[13] noted this, and have presented[14] a mass of evidence from the realm of physical science indicating the general distribution of radioactivity. It exists in air and soil, in spring-water, and in freshly fallen rain and snow. Potassium, one of the essential elements of

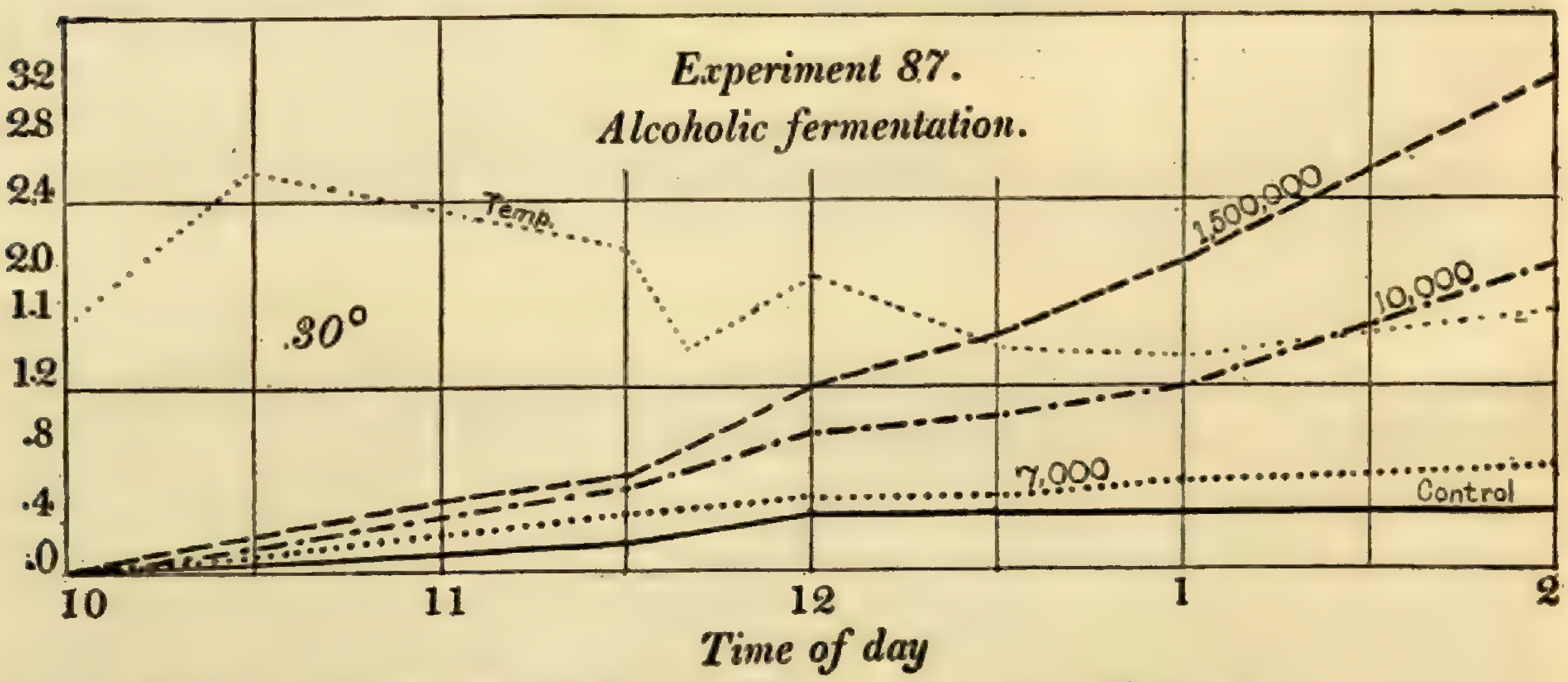

FIG. 12. Acceleration of alcoholic fermentation by radium rays.

plant food, has been found by Campbell to give off β rays,[15] and some evidence has also been found that calcium possesses the same property. The researches of many investigators have clearly demonstrated the general occurrence in nature of free negative electrons. These discoveries not only add to the interest and importance of the study of the physiological rôle of radium rays, but also point out the way for further investigation.

An arrangement devised by Mr. Hugo Lieber facilitated the study of the effect of a radioactive atmosphere on germination and growth. The apparatus is clearly shown in Fig. 13, and needs little further explanation, except to say that the hollow cylinder, R, has its inner surface coated with a Lieber's radium coating. The bell-jars fit tightly on to the ground glass plates, and a current of air is kept passing through the jars by attaching the tubing from the lower tubulure to an exhaust pump. The air passing through the radium-lined cylinder carried with it the emanation given off by the

[13] *Science*, N. S., **25**: 263. 1907.

[14] *Mem. N. Y. Bot. Garden*, **4**: Chap. II. 1908.

[15] *Proc. Cambridge Phil. Soc.*, **14**: 211. 1907. *Nature*, **76**: 166. 1907.

radium, and thus the plants were subjected chiefly to the influence of α rays.

In the experiment here described, dry seeds of timothy grass were sown on the surface of the soil in two pots

FIG. 13. Apparatus for growing seedlings in a radioactive atmosphere. Cf. Fig. 14.

and placed, one under each of the bell-jars. After five days, during which a continuous current of air was de-

livered over the cultures, the seeds were found to have germinated and grown uniformly under the control jar, but, in the culture exposed to the emanation, the seeds immediately under the funnel through which the emanation was delivered had entirely failed to germinate. The other seedlings of this culture were only very slightly less vigorous than those of the control (Fig. 14).

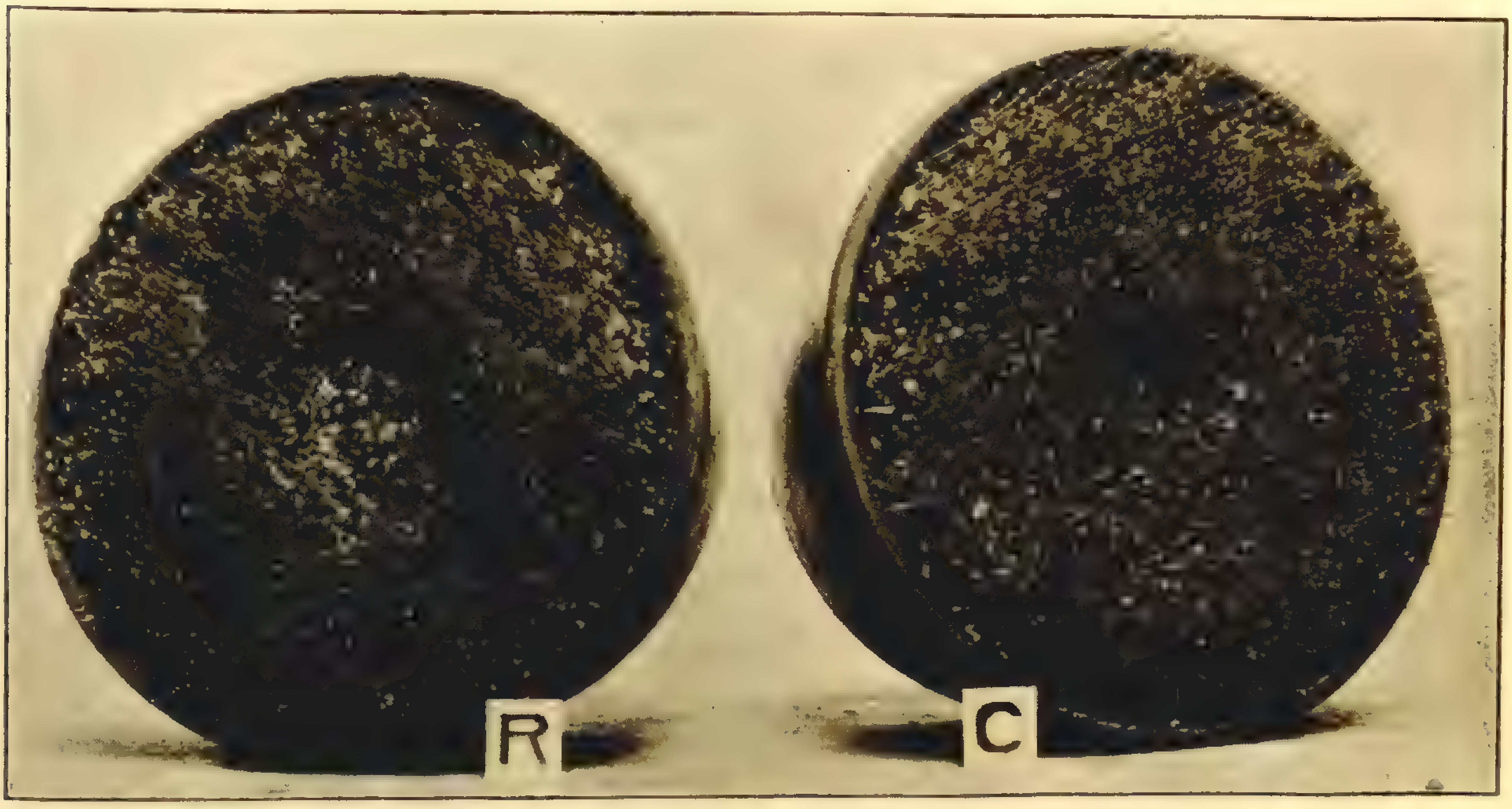

FIG. 14. Result of growing timothy grass in a radioactive atmosphere as shown in Fig. 13, R, exposed cultures; C, control.

To further investigate the effects of this radioactive air, five germinated seeds of *L. albus* with radicles over 10 mm. long were marked with India ink 10 mm. back from the root-tip. These seedlings were then suspended vertically, five under each bell-jar. The air, normal in one jar, radioactive in the other, was forced into the bell-jars by means of a rubber bulb, the blasts being given at irregular intervals of from two to twenty-four hours. At the end of the first twenty-four hours the average length of the exposed radicles was 19.00 mm., and of the control only 12.10 mm. At the end of the second twenty-four hours the average lengths were, for those exposed 23.30 mm., for those unexposed, 12.70 mm. The curves of growth for this experiment are given in Fig. 15, showing the acceleration in rate of growth under the conditions imposed.

The growth of roots was retarded in water exposed for twenty-four hours to the rays. The experiment was made as follows: Into 100 c.c. of tap-water, in which sealed glass tubes of radium bromide had lain for twenty-

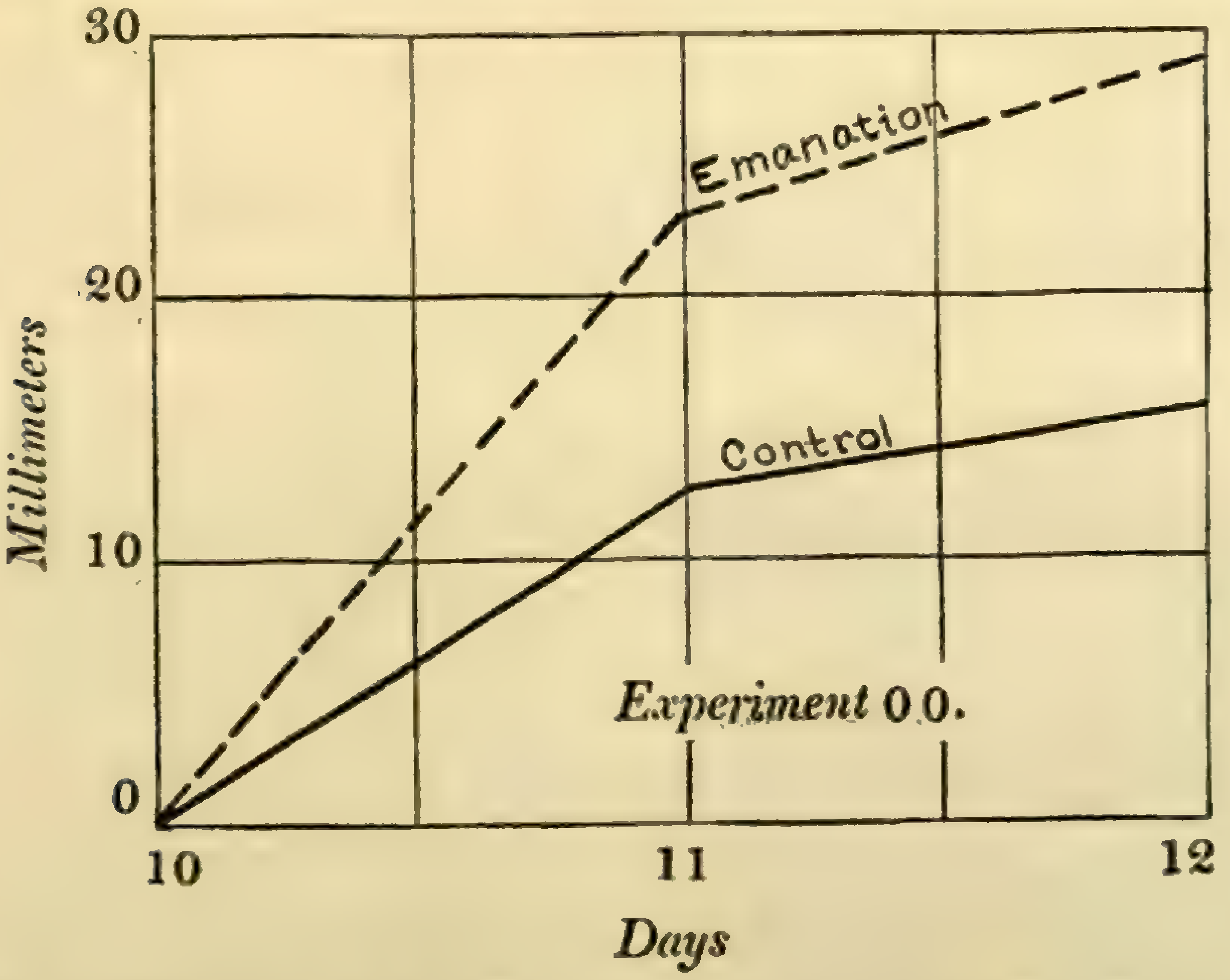

FIG. 15. Acceleration of growth of roots of *Lupinus albus* in a radioactive atmosphere.

four hours, the radicles of four germinated lupines were suspended up to an ink mark, placed 10 mm. back from the root-tip. Three cultures were arranged: A, with radium of 1,800,000 activity; B, with radium of 1,500,000 activity; and C, with no radium, serving as a control. At the end of five days the average lengths of the hypocotyls were, for A, 79.62 mm.; for B, 85.50 mm.; for C, 117.75 mm. The result, then, was a retardation of growth, in direct proportion to the degree of activity of the radium to which the water was exposed (Fig. 16).

Following up the suggestion in the discovery that freshly fallen rain is radioactive, several experiments were made with a view of ascertaining the effect of this radioactivity on plant growth. Rain-water was caught in the open, in chemically clean glass dishes, after about four hours of rain, so that the air was well washed. This water was kept carefully covered, for one month, when another opportunity presented itself of collecting another lot of rain under similar favorable circumstances. The

experiment was set up immediately after the last collection, using radicles of *Lupinus albus,* immersed to a measured length of 5 mm. in both the fresh and the stale water. Two parallel experiments, A and B, were run,

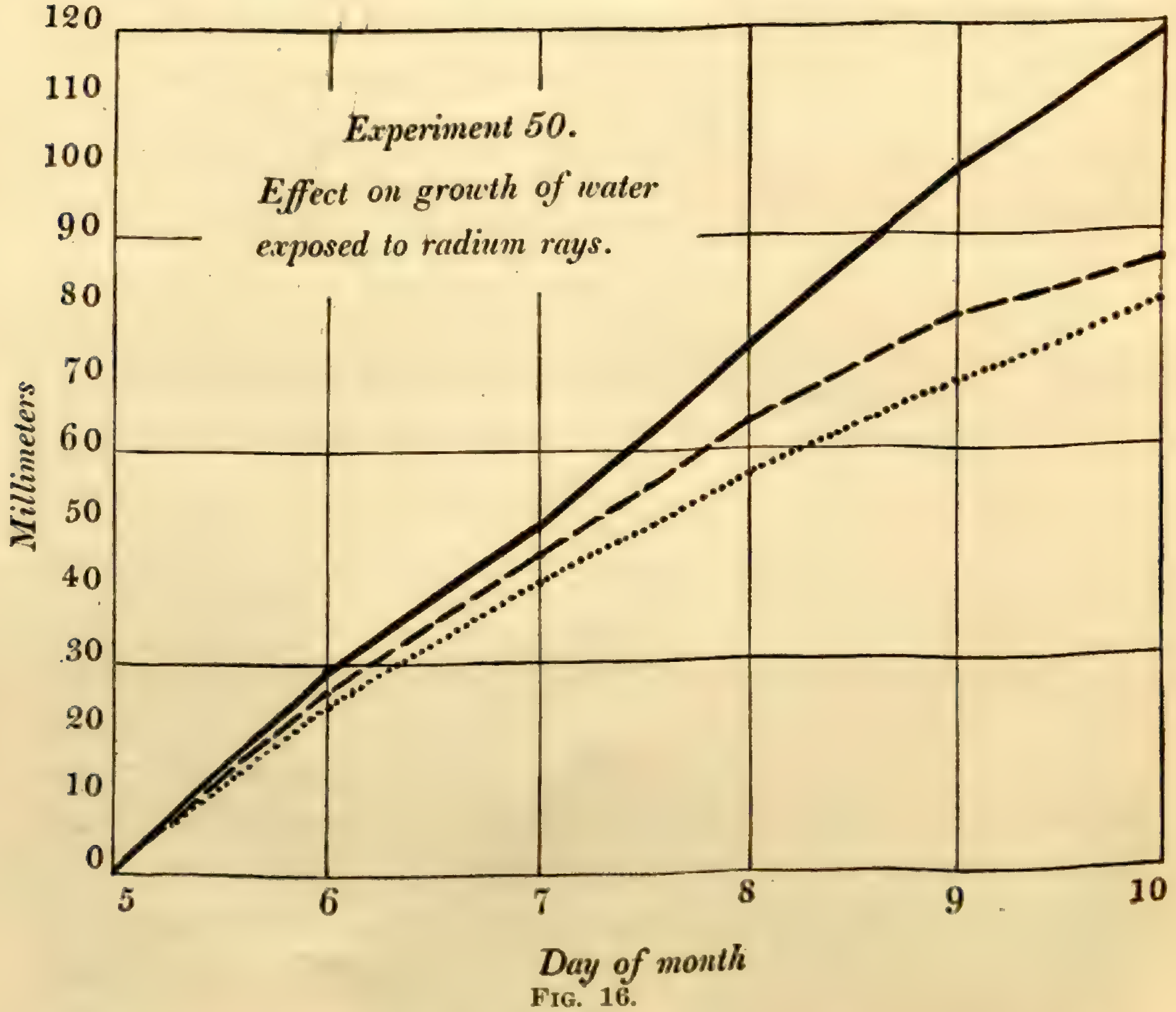

FIG. 16.

each with a "fresh" and a "stale" culture. At the end of 48 hours the lengths of the radicles averaged, for set A, 23.50 mm. fresh; 27.50 mm. stale: for set B, 22.38 mm. fresh; 27.00 mm. stale. The curves of growth are shown in Fig. 17. The experiments of which this is a type indicate that, as a result of its radioactivity, freshly fallen rain water tends to retard the growth of roots. We have as yet no data on the effect of this factor on the activities of the shoot.

Profound histological changes follow exposure to the rays. These effects are due chiefly to a disturbance of the normal functioning of the cambium, and are in harmony with results of experiments on animals, in which it has been shown that embryonic tissue is more sensitive

than any other. After an exposure of seeds under certain conditions, the cambium is frequently entirely lacking, all of the cells in the given organ having passed over into the mature state. The treatment appears to accelerate the approach of senescence.

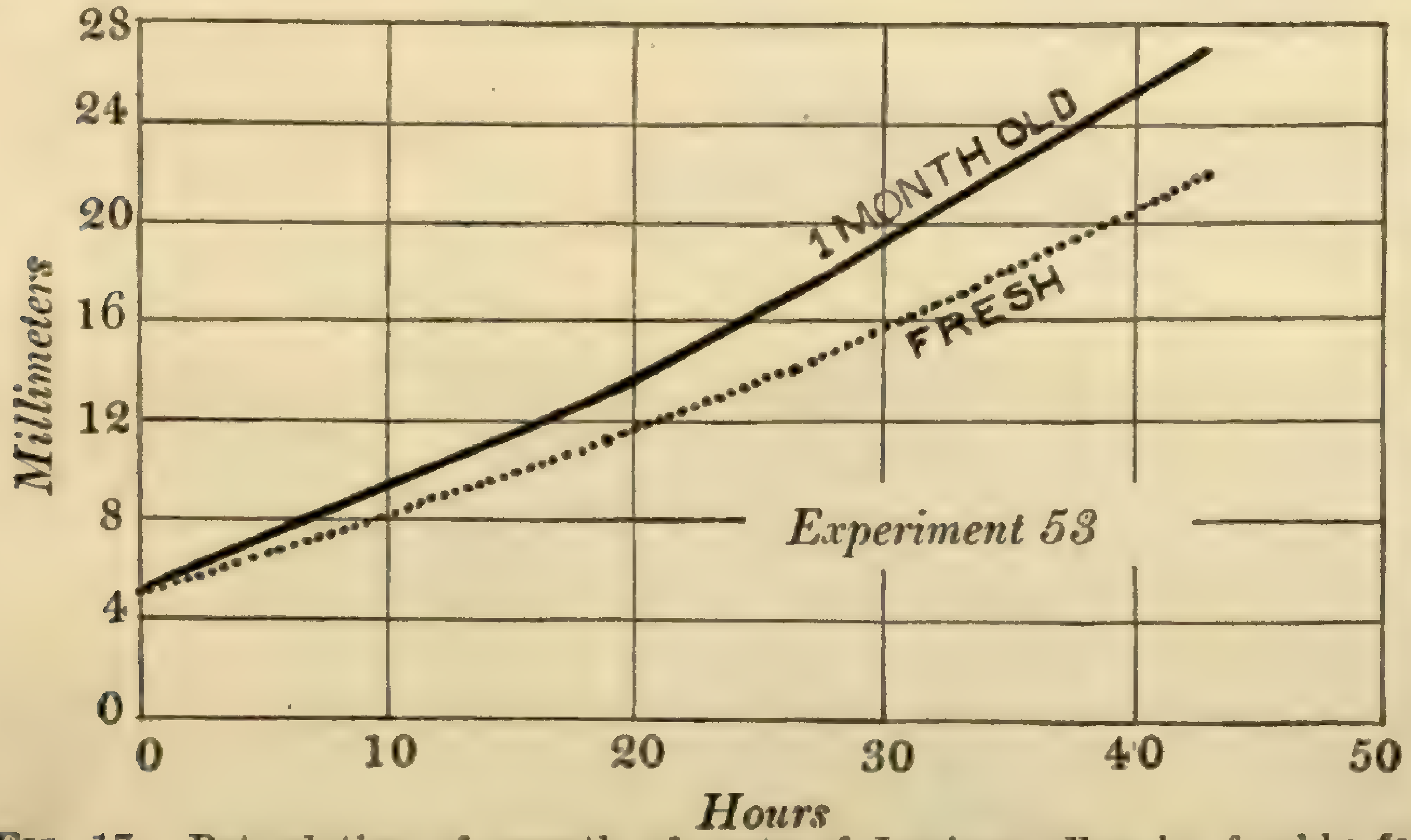

FIG. 17. Retardation of growth of roots of *Lupinus albus* by freshly fallen rain water. Cf. Fig. 16.

Exposure to the rays also induces marked irregularities in mitosis. This is shown, among other ways, by the failure of some of the chromosomes to take part in the organization of the daughter nuclei. Usually such chromosomes organize smaller, nuclear-like structures within the daughter-cells. In one instance they were observed to be undergoing an independent karyokinesis at one side of the main mitotic figure. Interesting possibilities are here suggested, along the line of experimental mutation.

Experiments like those described in this paper have been many times repeated with confirmatory results, and seem amply to justify the general conclusion, earlier stated, that radium rays are a stimulus to plant activities. The reaction to a stimulus between the minimum and optimum points is an excitation, or acceleration of the given process; the reaction to an over (superoptimal) stimulus is a depression, or retardation of function, and, if the stimulus is sufficiently intense, complete inhibition or ultimate death.

ON THE ORIGIN OF STRUCTURES IN PLANTS

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THE systems of organs of which a higher plant more especially is composed generally hold an intimate physical relation to one another. They are bound together so intimately by reason of their position in root or shoot that the growth, development or response to stimulus of one is in a very great measure molded by the growth, development or reaction of all the rest. In addition to these considerations, when the origin of tissues or of organs is being investigated, account must also be taken of the nutrition of the special organ as well as its especial relation to environment external to the plant of which it is an integral part. Thus the complex physical interrelations, and the physiological correlations as well, make the study of the functions, and behavior of the individual tissue, or organ, as a possible independent unit one of great difficulty. These general facts probably hold for plant tissues as a whole, but one system, namely, the trichomal system, offers a favorable field in which to study the origin, development and biological relationships of plant organs, inasmuch as it is comparatively little affected by other tissue systems. Beyond growing out of epidermal cells, remaining permanently attached to the epidermis, and deriving nourishment from the subjacent cells, the trichomes lead an independent existence, and in origin, development and form are not directly influenced, as the other tissues are affected, by the pressure of enveloping tissues, and in certain plants, as *Franseria dumosa,* the trichomes go one step further on the road to independence, in that they are chlorophyll-bearing and in a sense probably auto-trophic. For these and other

reasons the trichomes are favorable for the study of the origin of plant structures, as I recently found while working on certain hybrids, a detailed account of the results of which will be given in another place.

The walnuts, to which reference is made, bear 4 or 5 types of multicellular hairs, besides certain abnormal and one aberrant type. These are composed of 6, or 8 cells, or about 16 or about 32 cells. A close study of the development of the trichomes, in which mitotic figures were used as indicators of the course of cell division, showed the following to be facts: (1) In the earliest stages of development of all of the normal trichomes, the sequence of the first two, or three cell divisions was the same; (2), the sequence of cell divisions of the 6-celled and the 8-celled trichomes, during the entire development, is consistent; (3), the 8-celled trichome recapitulates faithfully the sequence of cell divisions of the 6-celled type up to the six-celled stage, and then adds two divisions in an order not departed from. Certain facts indicated that the late cell divisions of the two larger forms of trichomes, namely, those with about 16 and about 32 cells, do not hold to a sequence so closely, but further study of these difficult trichomes might modify this conclusion. These facts indicate that all of the multicellular trichomes may have originated in a common ancestral form and that by

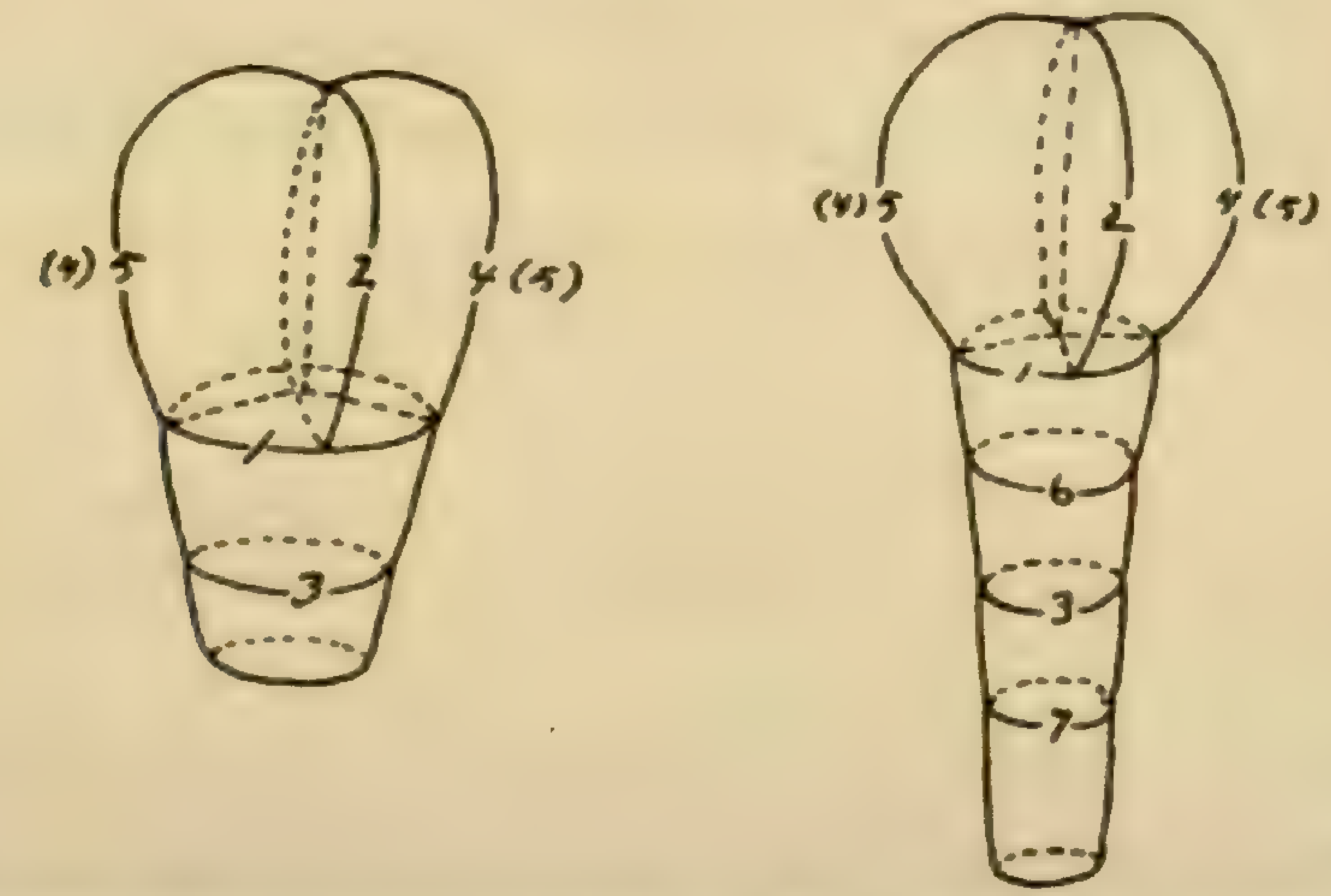

Fig. 1. Semi-diagrammatic sketches of 6- and 8-celled trichomes to show the Cell Lineage of each. The numbers refer to the sequence of the formation of the cell walls.

arrested development, or other differentiation, the various types of trichomes now to be found in Juglan's species have arisen. Certain of the trichomes are evidently more closely related to one another than to other types, and thus the trichomes are not all of equal age, but have been derived from an ancestral form at various times in the history of the plants which bear them. It is very probable, for instance, that the 6-celled type is more nearly related to the 8-celled type of trichome, than it is to either of the larger forms, but it would be difficult to say which represents the more ancient type. In development, and probably in origin, the types of trichomes thus behave as if they were separate organisms, or independent units of a complex organism. This is not the same as saying that each type of trichome is a "unit character," although certain observations which I have made on the distribution of trichomes in another plant, as well as the reversion of the trichomes in the second generation of *Juglans californica* × *Juglans regia* would justify this conclusion. Should it be the experience of other observers also that each type of trichome has its peculiar area of distribution in a plant, the conclusion that each form of trichome represents a separate unit character could not be avoided, and from such structural studies as above reported we should be able to trace their very origin as separate portions of the tissue of the plant.

In addition to the normal types of hairs in walnuts, as given above, there are also other types. Of such, there are certain abnormal forms which are evidently related to the already existing trichomes, of which they are slight modifications, and one aberrant type which is essentially different from these. The origin of the aberrant form was seen also, and was found to be as different from the mode of origin of the normal trichomes as the mature aberrant type is different from the mature normal form. In brief, its departure from the normal takes inception in the orientation of the first cell wall, which is longitudinal in place of being transverse as is usually the case (Fig.

2). Consequently it happens from this single initial deviation, there arises a form of trichome, unrelated to other existing types, and, consequently, of which it can in no wise be said to be a modification. In fact the new hair is a mutation, and its history shows in at least one way how such variation has its origin. In this instance there is no disappearance of intermediate forms of trichomes, since for structural reasons there can not be such.

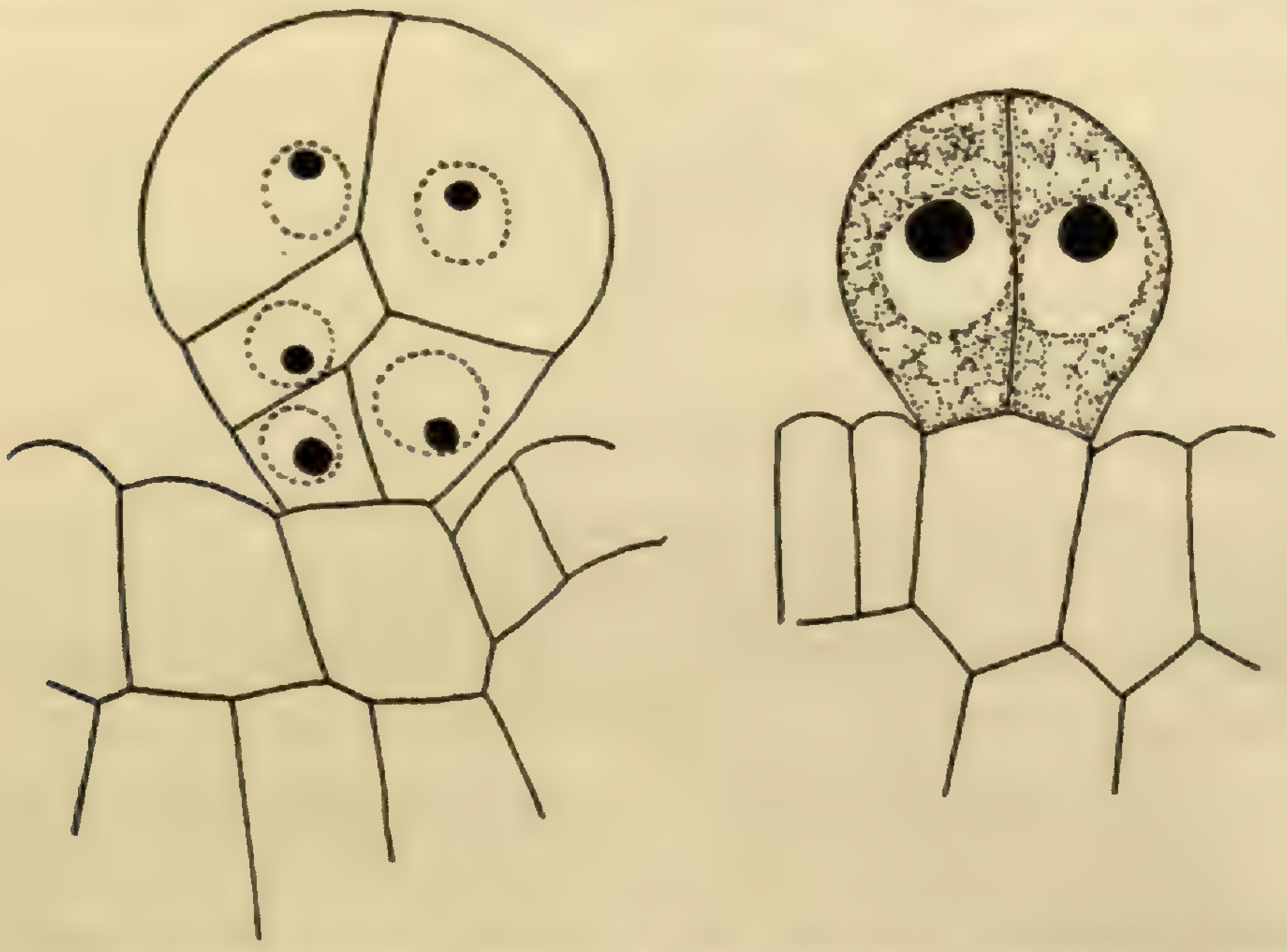

FIG. 2. Mature aberrant Trichome and two-celled aberrant Trichome, in which the first cell wall is laid down parallel to the long axis of the mature hair.

We therefore find in Juglans that the different types of multicellular trichomes may take their origin in one of two ways, namely, they may arise as modifications of types already existing in the plant, which is apparently the usual manner, or they may arise suddenly and hence provide points of departure for subsequent trichome formation and differentiation of which they would be the ancestral type.

The physiological reasons for the differentiation of the trichomes were not investigated, but observations indicate a close relation between size of hair and the position occupied by it on the plant member, and suggest that the factor of nutrition may be important in inducing certain, at least, of the irregularities noted.

THE ORIGIN AND FORMATION OF THE FROTH IN SPITTLE-INSECTS[1]

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During the summer months one observes upon trees, shrubs, herbs and grasses, numerous masses of froth-like material, which resemble large drops of spittle. An examination of a frothy mass soon discloses the presence of a small insect, greenish, brownish, or whitish in color, depending upon the species under observation. This is the immature nymphal stage of an insect belonging to the homopterous family Cercopidæ. So far as it is known, all the members of this family surround themselves with such a secretion, in which they spend their nymphal life. I have had under observation three species, *Aphrophora parallela* Say, *Lepyronia quadrangularis* Say, and *Clastoptera proteus* Fitch. Each of the species studied in this locality makes a characteristic froth, as may be easily recognized by a little study.

While there is much which has been written upon the production of froth by the insects of this group, the opinions of the many writers are very much at variance. This is especially true regarding the more recent literature on the subject. For this reason it seemed desirable to undertake a detailed study of this subject and to determine what organ or organs were concerned in the production of this secretion. This study consisted not only of field observations and laboratory experiments, but of a detailed study of the histological structures concerned.

This work was carried on in the Entomological Laboratory of Cornell University, and to its director, Professor J. H. Comstock, I am indebted for many courtesies. The problem was suggested by Dr. W. A. Riley, and to him I am indebted for constant aid and advice.

[1] Contribution from the Entomological Laboratory of Cornell University.

Historical

Gruner (1901) has given a very extended and excellent historical account of the work of individual writers on these insects. It is intended here merely to group the views held by the various writers, at the same time adding the opinions held by writers since the appearance of Gruner's paper.

As far as the writer has been able to determine from original sources, there are seven theories which have been advanced in explanation of the production of the froth. This does not take into account the belief of the southern negroes, who claim that the frothy masses are caused by horseflies, neither does it take into consideration the opinion formerly held by many, that it is the product of the stars, nor the view that it exudes from the ground.

Isidorus, who lived in the sixth century, is cited by Gruner as the first to write on this subject. He believed that the froth was the spittle of the cuckoo bird, and that from this secretion the cercopid spontaneously generated. Mouffet (1634) and other writers came to the same conclusion respecting the origin of the spittle and insect. Aldrovandi (1610), in his Ornithologia, strongly denies this assertion, but fails to enlighten the reader as to the true solution of the problem.

According to Gruner's account, Bock (1546) apparently believed that the froth was the product of plants and he gave a list of the plants producing it.

John Ray (1710) states that the spittle mass was caused by the insect found within the mass, and believed that it was expelled from the animal's beak. He was upheld in this view even in recent times by as prominent an authority as Uhler (1884). Fabre (1900) states that a clear fluid comes out of the beak and that to this fluid the insect injects air bubbles by grasping air with the last pair of lateral prolongations of the ninth abdominal segments.

Blankaart (1688) believed that the froth came out of the anal opening of the insect. In this view he is supported

by Poupart (1705), Frisch (1720), Geoffroy (1764), De-Geer (1773) and others. Morse (1900) modified this view somewhat in that he gives as his opinion that what comes out of the anus is a " clear somewhat viscid fluid " and that by means of appendages at the extreme tip of its abdomen the insect secured a moiety of air by grasping it, so to speak, and then instantly releasing it as a bubble into the fluid. Gruner (1900 and 1901) states that the fluid is exuded from the anus and passes under the body, flowing into a pocket-like space where it becomes impregnated with air which comes out of the stigmata located in the pocket.

Porta (1900 and 1901) believed that there were openings on the dorsum of Aphrophora which were connected with oval glands little distinct from the hypodermis. He describes them as arranged at the base of the excretory canal in numbers of five, six or even fewer, indistinctly separated from one another. To these glands he ascribed the function of producing the fluid. He also states that the bubbles are blown into the fluid by the method described by Morse.

Girault (1904) states that " during the process of secretion the fluid flows slowly from a point near the anal opening, and gathers between the legs, where, by their alternate agitation, it becomes mechanically mixed with air and forms cushions of air bubbles," and he further states "that the air is taken in at each up and down motion of the abdomen and that during this dipping process the ventral plates are in transverse motion like jaws, and that it is probable that the secretory glands are between them." From this we should infer that he thought that it came from special secretory glands and not from the anus.

Berlese (1907) believes that the froth is secreted by glands found upon the seventh and eighth abdominal segments, previously described by Batelli (1891).

In the following it is proposed to discuss the evidences bearing upon each of the current views presented above

and give in details the observations made to clear up the confusion.

Methods

The methods used in the biological observations are given in the body of the text. I refer here only to those used for the examination of the histological structures.

In preparing the tissues of the spittle insects for histological examination various methods of fixing, killing and staining were used. The best results were obtained by killing in hot water and then transferring immediately into Fleming's strong solution for twenty-four hours. Tissues killed directly in hot Fleming's fluid, while giving satisfactory differentiation of organs like the testes, intestine and fat cells, gave poor results with the glands. Very good results were obtained by killing in hot Gilson's fluid.

Good serial sections of the nymphs were obtained by infiltrating in paraffine 54° C., while adults imbedded in 62° C. paraffine gave better sections. Sections were cut from three to ten microns.

Staining was done on the slide with iron hæmatoxylin or Delafield's. Whenever the latter was used the tissues were counter-stained in eosin.

In order to get satisfactory preparations of the glands in surface view the tissues were killed in hot Gilson's fluid and allowed to stand for one half hour after having been opened and the fat carefully removed. After washing in seventy per cent. alcohol and a few drops tincture of iodine, the specimens were stained in borax carmine for a few minutes, dehydrated, cleared and mounted in balsam. Great care must be observed in teasing the fat away from the glandular region, otherwise the cells will be disarranged.

Personal Observations upon the Production of the Froth

I first studied the gross features of the froth formation in several specimens. A large specimen of *Aphrophora*

parallela was taken from the frothy mass and by means of a camel's hair brush was thoroughly freed from every particle of froth. The specimen was then placed upon a dry twig. It soon inserted its beak in the plant and gradually increased in size. It projected the tip of its abdomen extensively and then retracted it. This operation it repeated several times. Suddenly a small drop of a clear liquid appeared at the very tip of the abdomen, coming distinctly out of the anal opening. Observations made with a hand lens upon other parts of the body, especially in the region of the dorsum, failed to show any fluid whatever. The small drop was soon joined by another, and these in turn were followed by many others, the whole mass of fluid passing down on the ventral side of the body along the channel formed by the sternites and the prolongations of the pleurites (Figs. 1 and 6). Again, the fluid was noticed to be fairly oozing out of the anal opening. After a quantity had accumulated about the body of the insect, it was noticed that the last pair of legs, sometimes also the second pair, would reach out to the region of the seventh and eighth abdominal segments, then rub against the body and against one another as if in the process of mixing substances. After the fluid had been well mixed and the surface had been covered by it, it was next observed that the nymph moved the tip of the abdomen out of the liquid, opening up the pair of lateral appendages of the ninth abdominal somite, which immediately closed again. Then with a downward movement these parts were immersed in the liquid and the appendages, upon being opened, released a particle of air in the fluid. This operation was repeated many times, with the result that the insect was soon covered with air bubbles, which gave the characteristic covering a froth-like appearance. It was noticed that by changing the size of the air-grasping pocket, the insect is able to make bubbles of any size. For that reason, the bubbles in the smaller forms are always very much smaller than those of the larger spittle insects. It is partly this feature

which determines the above-noted characteristic appearance of the froth of the different species. The insect does not always wait until the body is completely covered with fluid before injecting the air into it.

In order to make sure that the larger portion of the fluid came only from the anus, the latter was closed by a plug of lens paper, which being capped with balsam, and then allowed to dry for a few moments, closed the anal opening perfectly. The insect, upon being placed on a twig, after locating a satisfactory place, soon pierced the plant with its beak and began feeding. It rapidly increased in size and became much distended and swollen. Although observed for over three hours not a single drop of fluid came out. In a specimen whose anal opening had not been carefully sealed a drop of liquid succeeded in coming out of the tip of the abdomen, on the side of the filter plug. Thus it was demonstrated, as any one who desires to repeat the operation may, that at least one of the constituents of the froth is emitted from the anal opening, and that the views of Mouffet, Porta, Berlese and Girault are not correct, for according to their interpretations the closing of the anus would not interfere with the production of the froth.

Histological Study of the Structures of the Glands of Batelli

While it is seen that the greater portion of the liquid from which the froth is produced is derived from the anus, there arises the question whether there are not other organs, the secretion of which may take a prominent part in the formation of the spittle.

In the pleural region of the seventh and eighth abdominal somites very large hypodermal glands are located. To the naked eye these glands are not easily discernible upon the nymph, their positions being detected only if there happens to be a large supply of their secretion. Under the hand lens when the abdomen is extended, there are to be noticed whitish patches, even when the secretion

has been completely removed. These, which lie in about the mid-pleural region, are somewhat pulvinate in shape, but by no means regular in outline.

As to the location of these glands there seems to be some difference of opinion. Batelli (1901) describes them as being located on the last two abdominal segments. Misinterpreting Wheeler's (1889) account of the adenopodia of the first abdominal segment in embryos of Nepa and Cicada, he erroneously homologizes these glands of Aphrophora with such structures, but rejects Wheeler's view that they are homologous with abdominal appendages. Porta (1900) and Gruner (1901) believed that these glands are situated on the seventh and eighth abdominal segments, while recently Berlese (1907) gave as his opinion that they were located on the eighth and ninth abdominal somites. I am of the opinion that Porta is correct, for there is no evidence that the first abdominal segment has been suppressed and they are clearly on the existing seventh and eighth abdominal somites (Fig. 2). Morever, this would harmonize more fully with Ber-

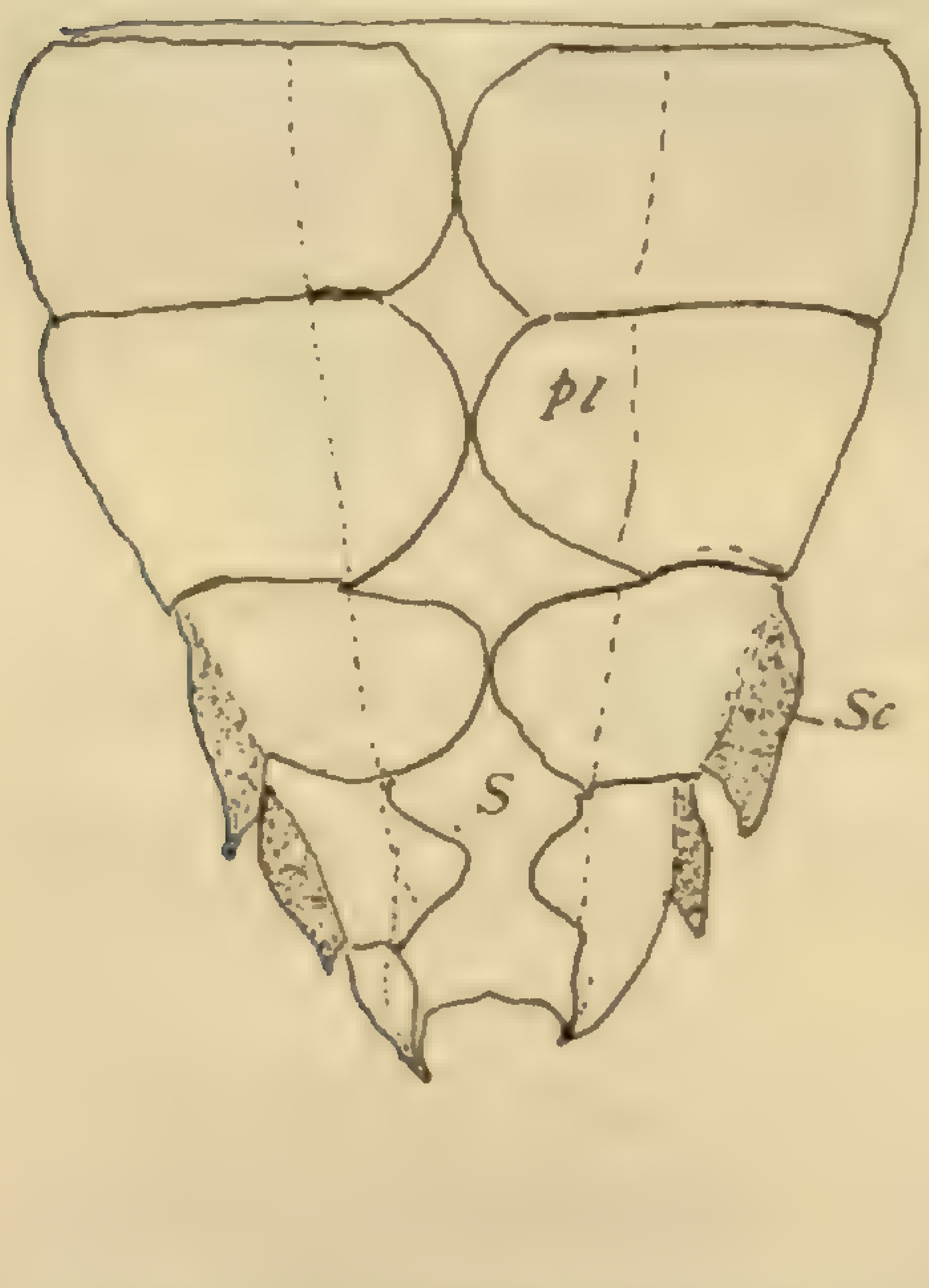

FIG. 1. Ventral View of full-grown Nymph of *L. quadrangularis*, × 40. *Pl*, pleural prolongations; *Sc*, secretion of the glands of Batelli; *g*, groove.

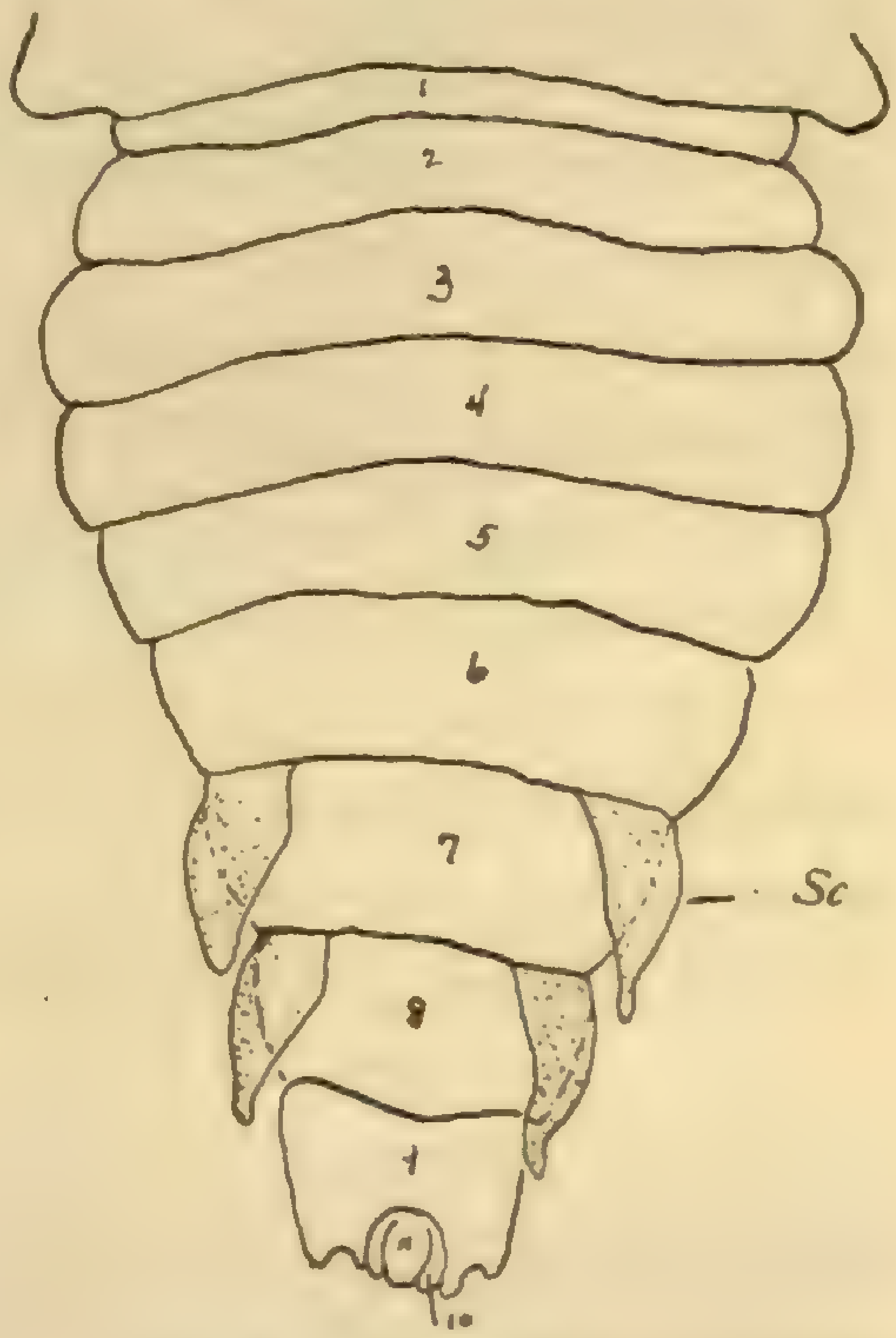

FIG. 2. Dorsal View of younger Nymph of *L. quadrangularis*, × 40. 1-11, tergites; *Sc*, secretion.

lese's own labeling of the segments in the abdomen of *Cicada plebeia* (*Gli Insetti,* Fig. 297, page 263).

An examination of the cuticle in the region of the seventh abdominal gland under the 3 mm. objective of the compound microscope shows that it is free from hairs, which are more or less abundant in other regions of the body. Under the one-sixteenth-inch oil immersion objective one is able to readily discern numerous minute pores (Fig. 3), giving it the appearance of very fine ingrained leather. These pores are more or less regularly distributed over the surface, equally distant from one another, and of equal size throughout the region. Similar pores were found on the eighth abdominal pleura. The most diligent search failed to reveal any such structures in any other region of the body. As I shall emphasize later, these are the openings of true cuticular pores through which the secretions of the underlying glands emerge to the surface.

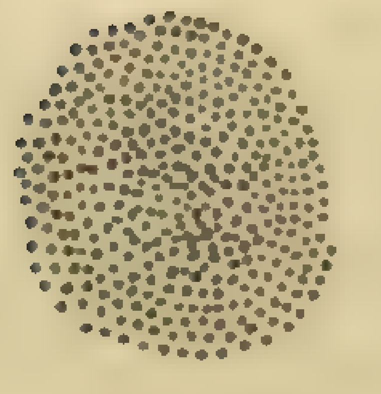

Fig. 3. Surface View of the cuticular Pores overlying the Glands of Batelli.

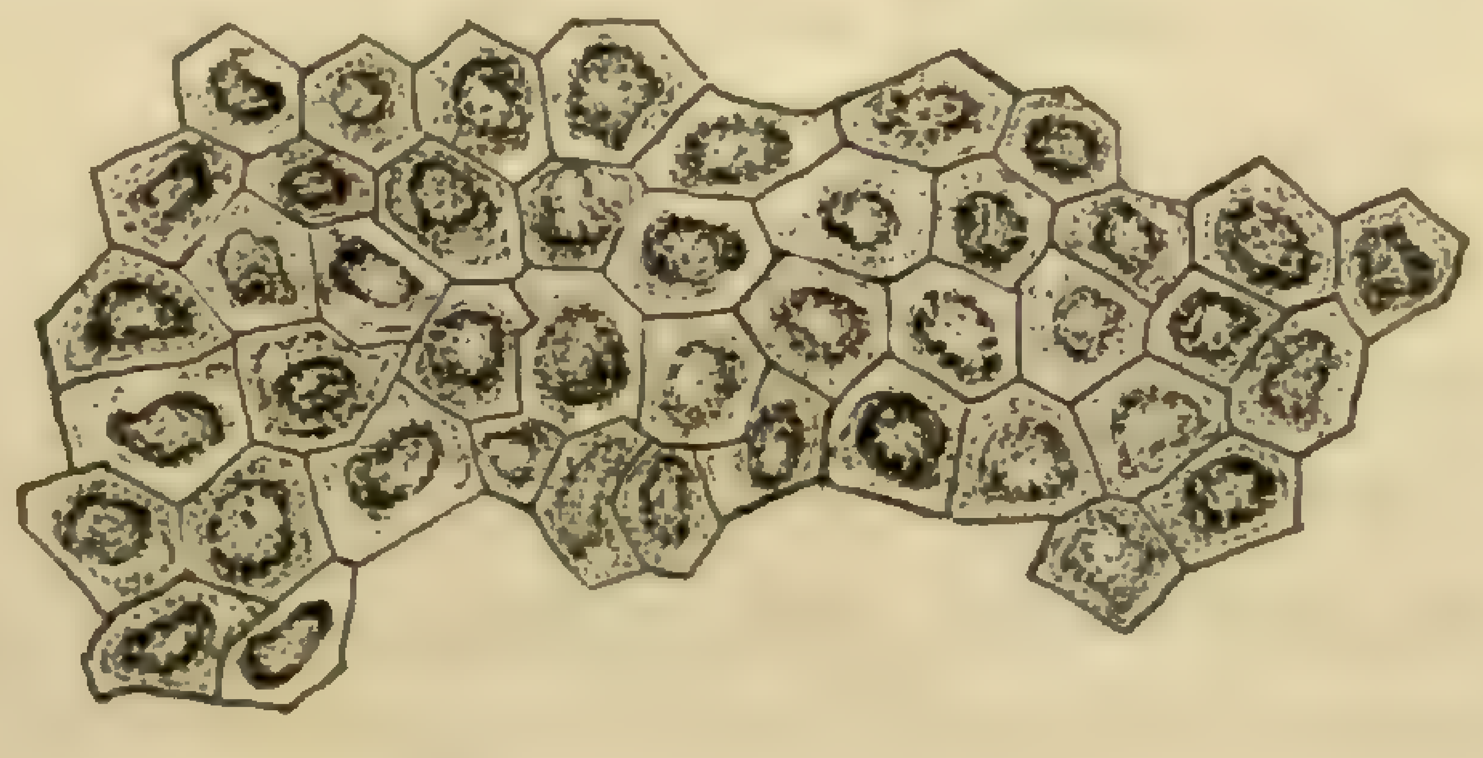

Fig. 4. Surface View of the Epithelium of the Glands of Batelli, × 250.

Specimens of the spittle nymphs were opened and the underlying fat carefully removed. Although it is difficult to separate the fat from this region without destruction of the glands, enough was removed so as to present a satisfactory area for study. The cells (Fig. 4) in good preparations were clearly defined, mostly hexagonal (occasionally pentagonal), though somewhat irregular from mutual pressure. They lie in close apposition to one another. The nuclei are large, round or oval, and in surface view appear situated in the center of the cell.

They are granular and occupy a large portion of the cell. The protoplasm in the region of the nuclei is highly granular and is readily stained. In the periphery of the cell it is not stained as readily, appearing somewhat hyaline. In some of the preparations made with specimens which had been killed in alcohol there were a number of intercellular spaces, while in the preparation of the glands which had been fixed immediately after removal of the fatty tissues such appearance was lacking, except in places where it was obviously due to mechanical cause. Arnhart (1906) gives a photomicrograph of a surface view of the wax-glands of bees, and explains these openings as tracheal in nature. Their presence is, in my opinion, due solely to faulty preparations rather than to the presence of any special tracheal ramifications. In general appearance the cells in surface view are very similar to those of the wax-glands of the honey-bee. A comparison with the excellent figures of Dreyling (1905) serves to bring this out clearly.

In longitudinal sections of *A. parallela* and *Lepyronia quadrangularis* the hypodermal cells of this region are greatly enlarged (Fig. 5), and strikingly resemble those

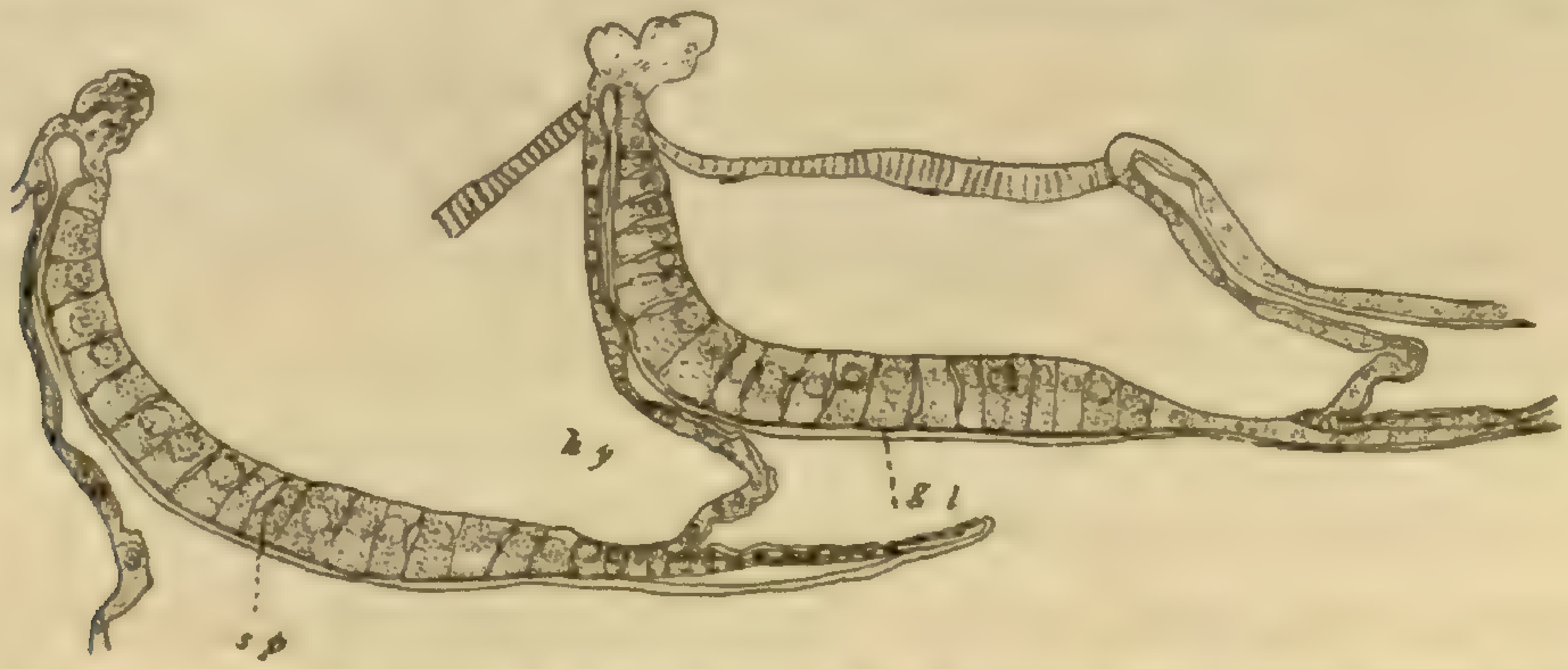

FIG. 5. Frontal Section of the Glands of Batelli in the Nymph of *Lepyronia quadrangularis*, × 125. *Gl*, glandular epithelium; *hy*, ordinary hypodermis of the body-wall; *sp*, spaces.

of the wax-gland of the bees. Each gland has the appearance of a curved band or bow, the central portion of which is thick, while it gradually tapers towards the ends. The same thing is noticed in the cross section (Fig. 6). This appearance is due to the general decrease in height of the

individual cells from the center to the periphery of the glandular mass. The cells in the main body are sharply defined, being separated from one another by distinct lines of demarcation. Near the margin of the gland it is not so easy, however, to define the contour of the individual cells, these passing gradually into the regular type

FIG. 6. Cross section of the seventh Abdominal Segment showing the Glands of Batelli, × 110. *Sg*, sternal groove; *pp*, pleural prolongations.

of hypodermal cells. In this type the nuclei are smaller and the cell outlines are not discernible. In sections of the gland the cells are not uniform in width, due to the fact that the sections pass in the center of some and in the sides of others. The glands of the two segments are about equal in size. In sections that pass through the long axis they are 292 microns in *Lepyronia quadrangularis,* and in *A. parallela* they are 465 microns. Most of the sections which the writer has made show clear spaces (*sp.,* Fig. 5) between the individual cells. These spaces vary in their appearance in different preparations, and evidently represent artifacts due to faulty fixation, rather, than the normal appearance of the cells.

In the middle of the glands the cells are high, cylindrical or cubical. On the margin they are low. In the last instar of the nymphs of *A. parallela* they are 30 microns in height and 18 microns in width in the center

of the gland, while in the margin the measurements are approximately 16 by 14 microns. The nuclei are round or oval and are situated in the lower margin of the cell. They are very granular and stain deeply. They are about 8 by 6 microns in dimensions. The protoplasm is highly granular, much more so in the region of the nuclei and in the margin underneath the chitin. The cuticula over the gland is about 8 microns thick, while that of the adjacent body wall is 12 microns.

If one makes satisfactory sections through the glands of these insects it is very easy to see extremely minute openings in the overlying cuticula leading from the glands to the surface. These outer openings correspond to those described above. For each canal there is a pore. Their distribution over the gland is regular. They are unbranched, perpendicular to the surface of the cells and about equally distant from one another (Fig. 7). As has

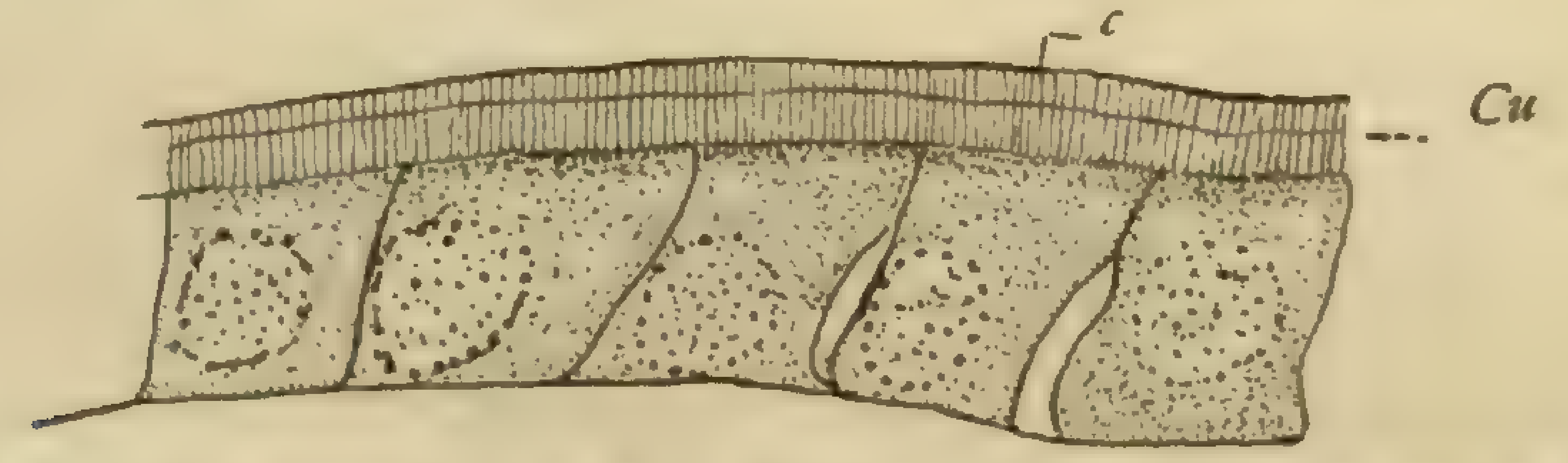

FIG. 7. Enlarged Portion of the Gland of Batelli, showing the cuticular canals, × 275. *Cu*, cuticula; *c*, canals.

been stated, similar pores do not occur in other regions of the body wall. Berlese (1907) and many other writers hold the opinion that true pores are never present in the chitin, and that substances are not conducted through the chitin by any such arrangement. Dreyling (1905), in a paper already referred to, figures and describes canals in the chitin overlying the wax cells of the social bees, and ascribes to these the function of conveying wax to the outer surface. Many writers agree with Dreyling in this view. My studies of the cuticula in the spittle insect convinces me that such true pores are present and they do serve as conduits in carrying the secretions of the underlying glands to the surface. It was noticed on several occasions that in specimens dropped in hot Flem-

ing's fluid the region of the glands was always immediately darkened, while the other parts were not so affected. This was evidently due to a more rapid penetration of the fluid at the point, or the staining of the secretion within the pores.

The above-described glands are also present in the imago, but in this stage they are very greatly reduced in size (Fig. 8) and show many signs of degeneration. The

FIG. 8. Gland of Batelli in adult Insect, ×200. *G*, gland; *h*, ordinary hypodermis.

high cylindrical condition of the cells noted in the nymphal stage is absent, and the sharply defined cell divisions are not present. The protoplasm is scanty and not so granular as in the nymphal stage. Many of the cells show signs of breaking down. Scattered throughout the glandular mass one finds many irregularly shaped bodies which are stained of a pinkish color by the eosin. No spaces were noticed between the individual cells. The nuclei are round and oval and of about the same size noted for the nymph. They show signs of breaking down, in fact some of them are surrounded by clear space, and many had a shrunken appearance.

FUNCTION OF THE GLANDS OF BATELLI

Morse (1900) states that "On the sides of the seventh and eighth abdominal segments may be clearly seen leaf-like appendages, which are possibly branchial in nature." These he figures and describes as "extremely tenuous and having the appearance of clusters of filaments, slightly adhering together and forming lamellate appendages similar to the gill-like appendages seen in the early stages of Potamanthus," though he admits they do not have the definiteness of these structures. Specimens he placed in

water lived for some time and he concludes that the above-referred to structures have a respiratory function. These so-called branchial tufts of Morse (*sc.*, Figs. 1 and 2) are nothing more nor less than the plates of secretion from the glands described above. This secretion is not filamentous, but appears rather very granular. It is very easy to remove these flakes of wax by means of camel's hair brush from the segments to which they adhere but slightly. The secretion is not soluble in alcohol and swells up after being allowed to stand in water for some time. It has a very striking superficial resemblance to beeswax.

The resemblance of these glands to the wax-glands of the honey bee, in the shape of the cells and in the location and appearance of the nuclei is very striking. This fact has already been pointed out by Batelli (1891), Gruner (1901) and others, who also find much in common with the cells of the wax-glands of coccids and other Hemiptera. Gruner (1901) thought that the *wax* served to line the "pocket" already mentioned so as to enable the air to penetrate it the better, and prevent the inflow of the fluid while the bubbles of air were being blown into the fluid. Porta (1900) accepting Morse's curious error regarding the presence of branchiæ, considered this thickened epithelium as a supporting structure for these supposed gills. Carrying further Batelli's misinterpretation of Wheeler's work, he regarded these "supporting structures" as homologous with the abdominal appendages of the embryos of Nepa and Cicada.

I am convinced that these glands secrete a mucilaginous substance which is utilized by the insect in the production of the spittle. Mixed thoroughly with the anal secretions it serves to render this viscid and thus to hold the air bubbles blown into it. This view is based upon the following experiments.

The region of the seventh and eighth abdominal segments of several specimens of the nymph was carefully

seared by means of a heated needle. These specimens were then placed on a plant and, although badly treated by the operation, soon found suitable places and began to suck up the juices, and as usual became enlarged. In the majority of cases each nymph began to emit drops of fluid from the anal opening. Although during the emission of this fluid the caudal segments of the abdomen were extended and retracted as in the normal specimen, in no case were bubbles formed within the secretion. This was true even after twelve to fourteen hours. In order to test whether this was due to the lack of some constituent normally secreted by the injured glands, air was blown into the fluid through a finely pointed tube; instead of being retained, none of the air balls remained in the fluid more than five to ten seconds. On the other hand, bubbles blown into the secretion of unseared specimens held in it for a very long time. This experiment was repeated many times over and always with the same result.

Other Supposed Sources of the Secretion

Besides these glands, other structures have been mentioned as participating in the formation of the froth, and in order to determine what part they played in it they were given careful consideration.

Berlese (1907) regards the glands of Batelli as the sole source of the secretion. This, my observations, confirming in part those of Morse and others, have shown conclusively to be incorrect. While I hold that the abovementioned glands contribute an important element to the spittle, there is not the slightest question but that the fluid portion is emitted from the anal opening.

We have seen that Porta (1900) considered the secretion as formed primarily by glands scattered among the hypodermal cells of the abdomen and opening to the surface through prominent canals, and that these were especially abundant in the region of the stigmata. All that could be noticed were the openings of trichopores.

A study of longitudinal and cross sections failed to show any such glands as described and figured by Porta. There are to be found the prominent oenocytes which are more numerous in the ventral surface of the animal. Berlese (1907) dismisses this view by stating that it is these oenocytes which Porta has mistaken for spittle glands. While this is doubtless in part true, I believe, as near as can be judged by the imperfect illustrations, that Porta was also misled by oblique sections through the body wall.

Porta (1900) mentions an oval gland which he says is situated in the fourth somite near the intestine, which he further states is ductless and has no connection whatever with the intestine or any other organ. He thinks that it may be concerned in the formation of the spittle, though he gives no tangible reason in support of this view. After careful study of a number of series of sections I failed to find any such independent gland and I am convinced that he in reality had under observation one of the cephalic glands and that of course it has no relation to the spittle secretion.

This same writer describes other glands which he considers are concerned indirectly in the production of the spittle. These he describes as being situated in the latero-ventral region of the third, fourth, fifth and sixth abdominal segments. He states that there are four pairs of these glandular masses, and in these ramify numerous tracheæ. He was unable to find any external openings to these glands and did not notice their connections with any other organs. The fact is that they are accessory reproductive organs, and that in perfect series their connection with this system may be most readily traced.

Summary

The secretion of the spittle insect is made up from two sources:

The fluid portion is the anal secretion into which the

insect by means of caudal appendages introduces numerous air bubbles.

The glands of Batelli secrete a mucilaginous substance which, added to the anal fluid, renders it viscous and thus causes the retention of the air bubbles.

The so-called branchial appendages of Morse and of Porta are merely plates of this mucilaginous secretion.

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SHORTER ARTICLES AND CORRESPONDENCE

PECULIAR ABNORMAL TEETH IN A JACK-RABBIT

About ten years ago I saw a curious malformation in the skull of a wood-chuck; the upper and lower incisors in some way missed coming in contact with each other in the usual way and had grown up and down through the skull and lower jaw, to wind and twist about above and below completely locking the jaws together. This animal was killed by a hunter near Waverly, N. Y., and is now in the Museum of Cornell University.

Since examining this first one, I have seen and heard of a number of similar malformations and in all cases the teeth of the upper and lower jaws grew more or less irregularly dorsally and ventrally.

A year ago at Claremont, Cal., another peculiar condition was brought to my attention in the skull of a young jack-rabbit (Figs. 1 and 2). In this skull the teeth are most remarkable

FIG. 1. Skull and one half of the lower jaw of a young jack-rabbit with unusual incisors. About half natural size.

FIG. 2. Skull from below and lower jaw from above of a young jack-rabbit with unusual incisors. About half natural size.

in the lower jaw, here the two incisors have grown nearly straight out some distance and are only slightly curved and twisted upon each other. In the upper jaw the incisors are not so long and only twisted at the tips.

WILLIAM A. HILTON.

POMONA COLLEGE, CLAREMONT, CAL.
June, 1908.

NOTES AND LITERATURE

ICHTHYOLOGY

Ichthyological Notes.—In the *Proceedings of the United States National Museum,* Volume 33, 1908, Jordan and Richardson give an elaborate review of the Flat-heads and Gurnards of Japan. In a personal letter, Mr. C. T. Regan, of the British Museum, makes one or two corrections in this paper, which may be noted here. The species called *Hoplichthys langsdorfii* by Jordan and Richardson is, according to Mr. Regan, a distinct species, not identical with the original *langsdorfii* of C. and V. The species called *Hoplichthys langsdorfii* by Jordan and Richardson may therefore receive a new name, "*Hoplichthys regani* Jordan and Richardson." The species called *Lepidotrigla microptera* is, according to Mr. Regan, distinct from the original type of that species, which is from Shanghai. The Japanese species should, therefore, stand as *Lepidotrigla strauchi* Steindachner.

In the same *Proceedings,* the same authors give an account of a small collection of fishes from the Province of Echigo, in northwestern Japan, obtained by a local naturalist, Masao Nakamura. Besides the three new species in this paper, the present writer has since received from Mr. Nakamura two other species never before taken in Japan, and which may be recorded here. These are *Podothecus sturioides* Guichenot, and *Dasycottus setiger* Bean.

In the same *Proceedings,* Eigenmann and Bean describe a collection of fishes from the Amazon River obtained by Professor J. B. Steere.

In the same *Proceedings* Mr. B. A. Bean discusses the forgotten genus *Ctenolucius,* a pike-like characin from Colombia.

In the same *Proceedings* Professor John O. Snyder describes a new sucker from the Santa Ana River, at Riverside, California, under the name of *Pantosteus Santa Anæ.*

In the *Smithsonian Miscellaneous Collections,* Volume 48, Mr. Barton A. Bean gives the history of the whale shark, *Rhinodon typicus.* The proper date of this genus is 1829.

In the *Smithsonian Miscellaneous Collections,* Volume 52,

Jordan and Branner give an elaborate account of the fossil fishes of the cretaceous beds of Ceará, Brazil, these specimens being obtained from the Serra do Araripe, the locality from which specimens had previously been obtained by Spix, by Agassiz and by collectors for the British Museum. These specimens are found in concretions of fine clay, and some of them are found to be beautifully preserved when these concretions are opened. In one species, *Calamopleurus cylindricus,* the black pigment at the base of each scale forming stripes along the side of the body is perfectly preserved, and the eye-ball is also well shown. In this collection Jordan and Branner find eleven different species, including all of those described by Agassiz, and including three new genera, Tharrhias, Enneles and Cearana. Most of the species belong to the family of Elopidæ, which represents one of the earlier types of bony fishes.

In the *Occasional Papers of the Boston Society of Natural History,* Volume 7, 1908, Mr. William C. Kendall gives a very useful list of the fishes of New England, and the localities from which each species has been recorded. The list contains 341 species, a number of these being estrays from the south brought northward by the Gulf Stream.

In the *Memoirs of the Carnegie Museum,* Volume 4, 1908, Jordan and Snyder describe and figure three new carangoid fishes from Formosa. One of these, *Ulua richardsoni,* constitutes a distinct genus, separated from Caranx by the extraordinary development of the gill-rakers, which cause the mouth to appear as if "full of feathers," much as in the genus of mackerels called Rastrelliger.

In the *Journal of the College of Science of the Imperial University of Tokyo,* Volume 23, 1908, Mr. Shigeho Tanaka gives a list of sixteen species new to the fauna of Japan, all but one of them new to science. Among these species is the new genus, *Owstonia,* of the family of Opisthognathidæ. Most remarkable of the discoveries is the addition of two more new species of Chimæra to the Japanese fauna. This makes eight species of Chimæra in all, described from Japan, all of them discovered since the year 1900.

In the *Annotationes Zoologicæ Japonenses,* Volume 6, 1908, Mr. Tanaka describes the fishes, sixty-three in number, collected by Professor Ijima in Sakhalin. Of the fauna of this region—

that of northern Japan—two new species, both of Porocottus, are described and figured.

In the *Proceedings* of the Academy of Natural Science of Philadelphia, Volume 59, 1908, Mr. Henry W. Fowler describes a collection of fishes from Melbourne. Among these is a new Chimæra, *Hydrolagus waitei,* for which a new subgenus, Psychichthys, is proposed. In the course of the paper a number of new subgenera are added to the already long list of genera of doubtful value.

In the same *Proceedings* Mr. Fowler has a catalogue of the lancelets and lampreys contained in the collection of the Academy of Sciences. A new genus and species, *Oceanomyzon wilsoni,* is described from the open Atlantic. *Lampetra æpytera* (Abbott) is said to be identical with *Lampetra wilderi,* the common black lamprey of Cayuga Lake. The name *Lampetra æpytera* has priority.

In the same *Proceedings* for 1906 Mr. Fowler describes new and little-known percoid fishes. He uses the name Dules in place of Kuhlia, and describes a new subgenus, Boulengerina, for *Kuhlia malo,* this group being based on the numerous gill-rakers. Some changes of nomenclature are made, based on the adoption of the rule that the first species mentioned in any genus shall become the type. This rule, which would have been just if it could have been originated earlier, will not be accepted by naturalists, as the International Congress has taken the view that in case a type is not fixed by the original author the writer following has a right to fix it, and once established it shall not be changed for any reason. The subgenus Astrapogon is suggested for *Apogonichthys stellatus,* characterized by the very long ventrals.

In the same *Proceedings* Mr. Fowler discusses the heterognathous fishes in the museum at Philadelphia, with descriptions and figures of many of these. Several new species are described, and a number of new generic and subgeneric names suggested.

These papers are subjected to critical review in the American Naturalist, Volume 41, by Dr. C. H. Eigenmann. Dr. Eigenmann claims that many of the new names proposed by Mr. Fowler are quite unnecessary. He says:

We must feel grateful to Dr. Fowler for his labor. But it is to be

hoped that in the future he will be more conservative in adding names to the science of ichthyology. The valid names do not compensate for the work imposed on some one else to separate them from the synonyms.

In the same *Proceedings* for 1907 Mr. Fowler catalogues the serranoid fishes in the collection at Philadelphia. He substitutes the name "Serranus" for "Epinephelus," for reasons that would be hardly valid even if we adopted the first-species rule, as Cuvier states that his name Serranus comes from the French name Serran, and that the species on which it is based are common in the Mediterranean. In other words, his actual type, although not the species first mentioned, by name, is *Serranus cabrilla.* The subgeneric Chrysoperca is introduced for *Morone interrupta.*

Serranus phæostigmæus is a species of *Epinephelus* described as new from Hawaii. A new species of *Alphestes* is described as *Epinephelus lightfooti* from San Domingo.

Eudulus is proposed as a new name for the genus Dules, which Mr. Fowler regards as preoccupied by Dulus, a genus of birds. Mr. Fowler shows that the number of the "Règne Animal," referring to these fishes, is prior in date to that number of the "Histoire Naturelle des Poissons" referring to the same species. Mr. Fowler also finds that the name malo of Valenciennes is older than that of mato given to the same fish—perhaps by typographical error.

The subgeneric name Callidulus is proposed for Centropristis or *Eudulus subligarius.*

In the *Annals of the Carnegie Museum,* Dr. Carl H. Eigenmann records a large collection of fishes from Paraguay. In all, two hundred and fifty-four species are known from that river basin. Ninety-five of these are peculiar to the Paraguay. One hundred and thirty-two are found also in the Amazon. The amazingly rich fish fauna of tropical America comprises one tenth of all known fishes.

In the *Proceedings of the Washington Academy of Sciences,* Volume 8, 1907, Dr. Eigemann describes a collection of fishes from Buenos Aires obtained by Professor W. B. Scott.

In the *Proceedings of the Field Columbian Museum,* Volume 7, 1907, Dr. S. E. Meek gives notes on fresh-water fishes obtained by him and others from Mexico and Central America. *Cichlasoma milleri* is described as new from Guatemala, and also *Rhamdia regani, Platypœcilus tropicus* and *Pœcilia tenuis.*

In the same *Proceedings,* Volume 7, 1908, Dr. Meek gives an interesting account of the "Zoology of the Lakes of Guatemala."

In *Science,* Volume 27, 1908, Professor J. O. Snyder discusses the region of the fauna of the Russian River in California, showing that these fishes were derived from the Sacramento River by a process of stream-robbing, by which through erosion the Russian River Valley incorporated small streams from tributaries of Clear Lake, which drains into the Sacramento.

In the *Bulletin of Agriculture of the Dutch East Indies,* Volume 8, 1907, Dr. P. N. van Kampen describes two of the mackerel found on the coast of Java. These descriptions are useful, but the synonmy given perhaps needs verification. These mackerel apparently belong to the genus Rastrelliger, distinguished from Scomber by the very great number of gill-rakers, recently described by Jordan and Starks.

In the *Annuaire of the Museum of Sciences of St. Petersburg,* Volume 12, 1907, Dr. L. Berg describes the grayling of Siberia, with a comparative account of their relation to other salmoninæ. The species known as *Brachymystax obtusirostris* from Siberia is made the type of a new genus, Salmothymus, differing from Brachymystax in having the vomer prolonged, with two rows of teeth, as in Salmo. The subgenus Thymalloides is proposed for *Thymallus arcticus,* this group species including also all the American grayling, the name Thymallus being restricted to *T. thymallus,* the grayling of Europe, which does not occur to the eastward of the Ural Mountains. Three species of Hucho are recognized, *H. hucho* in the Danube, *H. taimen* in Siberia and *H. perryi* in Japan. The genus Phylogephyra is recognized for *Thymallus brevirostris,* or *altaica,* of Siberia. This is distinguished by the larger mouth and larger and more numerous teeth, which are present on the head of the vomer and on the tongue.

Dr. Theodor von Kawraysky has published an elaborate account in Russian and in German of the sturgeons of the Caucasus, with lists of other fishes taken in the same region.

In the *Memoirs of the Museum of Comparative Zoology of Harvard* Dr. Charles H. Gilbert gives an account of the lantern fishes collected by the *Albatross* in the South Seas. The species obtained are carefully described, and their synonymy very fully worked out. Several new species are contained in the collection.

The genus Zalarges of Jordan and Williams is identified with Vinciguerria.

In the *Bulletin of the Museum of Comparative Zoology* for February, 1908, Mr. Samuel Garman describes a number of new sharks and skates. The genus Aëtomylæus is proposed for *Myliobatis maculatus. Raia kincaidii* is described as new from Friday Harbor, Puget Sound, and *Chimæra barbouri* from Aomori, Japan.

In the *University of Colorado Studies,* Volume 5, No. 3, Professor T. D. A. Cockerell gives a list of the fishes of the Rocky Mountains, with useful notes on geographical distribution, and references to the fossil as well as to the living forms recorded from that region. Brief keys are given, enabling local students to identify specimens in hand.

In the *Zoologischen Anzeiger,* Volume 32, 1908, Dr. Franz and Dr. Stechow describe an interesting case of symbiosis between the fish, *Minous adamsii,* a form of scorpion-fish, and the hydroid polyp Podocoryne from Sagami.

In the *Sitzungsberichte of the Academy of Vienna* for 1908 Dr. Steindachner describes two new fishes from Brazil.

In the *Transactions of the Wisconsin Academy of Sciences,* Volume 16, 1908, George Wagner gives a useful list of the fishes of Lake Pepin, forty-four species being recorded.

In the *Natuurkundig Tijdschrift of the Dutch East Indies,* Volume 67, 1908, Dr. P. N. van Kampen has an interesting series of notes on the spear fishes found in Java. The common species he identifies as *Tetrapturus brevirostris. T. mazara* of Japan may be the same species.

In the *Bulletin of the Société Nationale d'Acclimatation of France* Dr. Pellegrin gives a review of the fresh-water fishes of Madagascar, with discussions of the economic value of each species.

Among the papers left at the death of Professor Karl Ernst von Baer is a biography of Cuvier which had never been published, and which is exceedingly interesting as a contemporary account of one of the greatest of naturalists and written by one of his ablest contemporaries. It is published in the *Annales des Sciences Naturelles,* in Paris, by Professor Ludwig Stieda, of Königsberg.

In the *Archivos do Museu Nacional of Brazil,* Volume 4, 1907. Dr. Alipio de Miranda Ribeiro continues his catalogue of the

fishes of Brazil, this volume treating of the sharks, with descriptions of each species, and analytical keys. The memoir is beautifully printed and illustrated by photographs of very many of the species. The synonymy is given in an appendix, and the nomenclature is in general in accord with the rules adopted by American naturalists and by the International Congress.

Dr. C. T. Regan continues the catalogue of the fishes of Central America. *Brycon guatemalensis* is described as new from Guatemala. *Tetragonopterus macrophthalmus* is described from southern Mexico, as is also *T. angustifrons.* Mr. Regan recognizes a number of additional species of Lepidosteus. It is very desirable that the garpikes of the United States should receive a critical review. It is quite possible that more species really exist than the three which have been recognized by Jordan and Evermann. Mr. Regan proposes the name Conorhynchichthys in place of Conorhynchus, the latter name being preoccupied. This paper completes the study of the fishes in the fauna of Central America. It is a very important and very well executed piece of systematic work.

In the *Transactions of the Linnean Society of London,* Mr. Regan gives an elaborate account of the fishes collected by the Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner. One hundred and eighty-five species were obtained, many of them new to science, these being figured in the present volume. Among other interesting forms are six new species of the genus Champsodon.

Under the head of "Edible Fishes of New South Wales," Mr. David G. Stead, naturalist of the Board of Fisheries at Sydney, gives a popular account of the fishes which appear in the markets of Sydney, illustrated by numerous photographs. This interesting and valuable report is accompanied by a map of the state of New South Wales.

Under the title of "Trout Fishing in New South Wales," Mr. Charles Thackeray, of Sydney, gives an account of the various streams in the state, in which trout from Europe and the United States have been introduced. The little volume is extremely valuable to Australian anglers, and is also interesting as showing the remarkable success which has attended the introduction of the California rainbow trout in the Antipodes.

Under the head of "Guide to the Gallery of Fishes in the Department of Zoology of the British Museum (Natural His-

tory)," the trustees of the British Museum have published a book of two hundred and nine pages giving an account of the principal kinds of fishes, the characteristics of the different families, and in general an outline of the classification adopted in the distribution of the species in the museum. A number of figures are given, some of living and some of extinct species.

In the *Transactions of the Royal Society of Canada* Dr. J. F. Whiteaves continues his account of the fossil fishes of the Devonian Rocks of Canada, with descriptions of numerous species and restoration of others. Most interesting is the extraordinary *Bothriolepis canadensis,* restored in accordance with investigations of Professor Patten. This form has many characteristics of arthropod animals. With its head, eyes and coat of mail, suggesting something like a horseshoe crab, it is hard to believe that it is a fish. On the other hand, it is hard to believe that the tail, provided with what seems to be a rayed dorsal fin, can belong to any kind of crab-like animal.

In the *Sitzungsberichte of the Academy at Vienna,* Volume 116, 1907, Dr. Viktor Pietschmann describes two new sharks from Sagami Bay, Japan, *Centrophorus steindachneri* and *Etmopterus frontimaculatus.*

In the same journal for 1908 Dr. Steindachner describes fishes from South America, and also a loach from Formosa, the latter called *Homaloptera formosanum.*

In the same journal, Dr. Steindachner describes a new genus of characins called "Joinvillea."

In the same journal he describes also other species of South American river fishes.

In the *Annals and Magazine of Natural History,* 1908, Mr. Regan describes new fresh-water fishes from Japan and Formosa.

In the same journal Mr. Regan describes also new fresh-water fishes from New Guinea.

In the *Proceedings of the Zoological Society of London* Mr. Regan describes a number of new species from Corea.

In the *Annals of the Natal Government Museum* Mr. Regan gives a list of marine fishes from South Africa, nine of them being described as new. Mr. Regan gives also a useful analysis of the eight species recognized by him in the genus Squatina. Of these *S. japonica* and *nebulosa* are found in Japan, and *S. californica* off the coast of California.

In the *Annals and Magazine of Natural History,* 1908, Mr.

Regan gives a synopsis of the sharks, Scylliorhinidæ. To Scylliorhinus are referred the species of Catulus, Cephaloscyllium and Halælurus. The genus Parmaturus is regarded as identical with Pristiurus.

In the same journal, Mr. Regan has a review of the sharks of the family of Squalidæ. In this the name Spinax is preferred to Etmopterus, because of the inaccuracy of Rafinesque's description. *Frontimaculatus* of Japan is regarded as identical with the European *E. pusillus.* The genus Zameus is regarded as identical with Scymnodon. Deania and Lepidorhinus are placed in synonymy with Centrophorus. *Deania eglantina* from Japan is regarded as identical with the European *Centrophorus calceus.* The name Scymnorhinus is preferred to Dalatias, because of the very inaccurate description of the genus of Rafinesque.

In the same journal Mr. Regan describes new loricaroid fishes from South America.

In the same journal Mr. Regan gives a synopsis of the cestraciont sharks. He regards the name Heterodontus as preoccupied by Heterodon, thus accepting the latter name Cestracion. He accepts the genus Gyropleurodus as distinct from Heterodontus.

In the same journal Mr. Regan describes *Cichlosoma lauræ* as a new species from Tampico. *Enneanectes carminalis* was found at Swan Island, near Honduras—a little blenny hitherto known only from Mazatlan.

In the same journal Mr. Regan describes a hybrid between the bream and the rudd, with notes on other hybrids among the European cyprinoid fishes.

In the *Proceedings of the United States National Museum* for 1908, Jordan and Dickerson give an account of fishes obtained by Dr. Jordan at Fiji. The fauna of the islands is essentially like that of Samoa, the physical nature of the reefs being closely identical in the two regions; but even in this small collection are several species which are distinctively characteristic of the New Guinea waters. The deep-bodied mackerel of the Pacific are separated from Scomber to form a new genus, Rastrelliger, differing especially in the very long gill-rakers, the mouth looking as if "full of feathers." With this are other characteristics, the teeth being very minute and there being none on the roof

of the mouth, and there are certain peculiarities in the structure of the bones connecting with the tongue.

In the "Actes de la Société Linnéenne de Bordeaux," 1907, Dr. Pellegrin describes a collection of fishes taken on the west coast of Africa, with useful notes as to their distribution. The nomenclature adopted is rather outworn, and not much notice is taken of questions of priority of names. The illustrations are photographs, very obscurely printed. It may be noted that *Sardinella aurita,* type of the genus Sardinella, is a large-scaled herring of the group called Harengula. The name Sardinella has priority over Harengula, and the name Sardinia must be used for the true sardine.

In the *Comptes rendus* of the French Association for the Advancement of Science, Dr. Pellegrin gives an interesting account of the incubation of the eggs of marine cat-fishes. The male takes care of the egg and the young, taking into the mouth from ten to twenty eggs. The young are retained in the mouth until the yolksac is absorbed. During this period of incubation the male does not feed.

In the *Annals of the New York Academy of Sciences,* Dr. R. W. Tower discusses the production of sound in sciænoid and other fishes. In this very lucid paper it is shown that these fishes "known as drums, croakers or roncadores" have specific drumming muscles, superficially attached to the swim-bladder. For this muscle Dr. Tower proposes the name *musculus sonificus.* The cause of the drumming or grunting noise is the contraction of this muscle, which produces a vibration of the abdominal walls and organs, especially the swim-bladder. In the sciænoid fish, the mechanism is adapted to the production of rapidly repeated sounds or rolls. In other fishes which grunt, as the sea-robin and toadfish, the muscles are intrinsically connected with the swim-bladder, and are known as intrinsic muscles. These muscles produce a vibration in the walls of the swim-bladder which may be repeated at intervals. Dr. Tower gives a number of valuable plates showing the structure of these organs, and also a graphic record of the sounds produced.

In the *Proceedings of the Biological Society of Washington,* H. Walton Clark describes the Plankton of the Lakes of Guatemala.

In the *Bulletin of the American Museum of Natural History,* Volume 25, Dr. L. Hussakof gives a catalogue of the fossil fishes

contained in the American Museum, with figures of many of the fragments.

In the *Biological Bulletin*, Volume 13, Mr. Fernandus Payne describes the effect of light on the blind fish of the Mammoth Cave. In this species the fishes turn away from the light. The young are more sensitive than the adult. The young deprived of eyes are as sensitive as those which have them. They seem to be equally sensitive on all parts of the body, and more sensitive to intense light. They seek the dark without regard to the direction of the rays.

In the Bureau of Fisheries, document 622, Mr. Irving A. Field discusses unutilized fishes, and methods by which these waste species can be rendered of economic service.

In the *American Journal of Anatomy*, Mr. William F. Allen describes the blood-vessels in the tail of the garpike, this paper being a continuation of his series of studies of the circulatory system in different fishes.

In the *Procedings of the American Academy of Arts and Sciences*, Dr. G. H. Parker describes the sensory reactions of the lancelet. This creature possesses in potentia the sense organs of the vertebrate. It is simple in structure, containing forerunners of the lateral-line organs, the ear, the temperature organs, and doubtless the forerunners of the rod- and cone-cells of the vertebrate retina. It is only slightly sensitive to light, but is sensitive to temperature and to sound.

In the *Journal of Experimental Zoology*, Mr. H. H. Newman describes the relation of the hybrids of *Fundulus majalis* with *Fundulus heteroclitus* to problems in heredity. The writer thinks that the study of development and heredity are identical, except that the latter is comparative. No two organisms start out from identical germ cells, nor do they ever develop under identical conditions. Instead of a fixity of relationship between pure strains and hybrids, there is constant flux.

In the *Proceedings of the United States National Museum*, Volume 33, for 1907, Seale and Bean describe the fishes collected in the Philippines by Major Mearns, with seven new species.

In the *Smithsonian Miscellaneous Contributions*, V, 1908, Mr. W. C. Kendall shows that the unrecognized species of whitefish from Saskatchewan River called *Coregonus angusticeps* by Valenciennes is the chub, *Platygobio gracilis*.

In the same *Contributions*, Dr. Jordan shows the identity of

the fossil stickleback from Nevada, *Gasterosteus leptosomus* Hay, with *Merriamella doryssa.* The species stands as *Gasterosteus doryssus.*

In the same *Contributions,* Dr. Gill gives an account of the habits of the miller's thumbs or blobs. He shows that *Uranidea* can not be maintained as a genus distinct from *Cottus* and that the common species must be called *Cottus richardsoni,* not *C. ictalops.*

In the *Transactions of the Wisconsin Academy of Science,* Mr. R. H. Johnson discusses the variations in number and size of the pylone cæca in Sun-fishes. In each species a variation of two or three was found. Thus in species as the rock bass, having on the average eight cæca, the number ranges from six to nine. In the calico bass, with nine, the number ranges from eight to eleven. DAVID STARR JORDAN.

THE INHERITANCE OF SEX IN HIGHER PLANTS

Digest of Professor C. Correns's Memoir[1]—It is stated in the preface that there is given here a more detailed reiteration of a report made September 18, 1907, to the united sections for zoology and botany of the German Naturalists in Dresden. Experiments in cross-breeding closely related species of plants of different sexual type, carried on since 1900, led to such remarkable results that an account was long withheld. When a repetition of experiments yielded like results, and a reconsideration of the deductions made revealed no flaws, conclusions were announced. For the plants examined the results are regarded decisive; but their wider application must be ascertained by further investigation.

Correns refrains from an historical review of the literature and attempts merely to present some new facts and relate them to previous facts. He does not wish, nor does he claim to be able, to construct a new theory regarding the nature of sex. He believes that there is much in common between his results and those reported by E. B. Wilson for Hemiptera. Finally he explains that by "anlage" of an organ as used in his paper he does

[1] "Die Bestimmung und Vererbung des Geschlechtes nach neuen Versuchen mit hoheren Pflanzen." Abstract presented before a recent meeting of the Medico-Biological Journal Club of the University of Virginia, by H. E. Jordan, adjunct professor of anatomy.

not mean the earliest visible developmental stage, but the representative of the organ in the germ-plasm.

In the introduction Correns notes that the present opinions concerning sex-determination are built largely upon the results (chiefly negative) obtained from attempts to control or alter sex, and upon observations on parthenogenetically developing eggs; in part also upon morphological and statistical data. The main object of his paper is to describe attempts to discover by experimental methods, whether the germ-cells have from the beginning a fixed sex-tendency and if so of what kind, and what rôle fertilization plays in sex-determination. He regards these as fundamental questions which must be answered before one can judge intelligently of the effects of unusual external influences. For the elucidation of these same questions he believes we are largely limited to the plants, particularly the flowering plants, due to the more favorable material they offer for experimentation.

In essence, the fertilization process in plants and animals is the same: two germ-cells unite to form a new organism. Botanists are to-day convinced of the polyphyletic origin of plants and, while it is possible, it is not very probable that sex-determination and sex-inheritance were arrived at in the different groups by the same path of differentiation. A question to be settled by further work, therefore, is whether the principles determined for the particular flowering plants under consideration apply also to other groups of plants, and also to animals.

Already in mosses are found a sharply expressed differentiation of germ-cells into egg-cells and sperm-cells, and this specialization is retained with various slight modifications throughout all the higher groups. In phylogenetically lower forms than the mosses the gametes are all alike (swarm spores). Chance or chemotactic influences may bring such into contact and subsequent union, or they may germinate asexually as in Protosiphon according to Klebs. Externally all are alike. Sometimes, as observed by Klebs in Chlorocytrium, cells from the same mother-cell may copulate. The question arises whether they are intrinsically alike or whether they consist of two classes, + and —, as Blakeslee proposes. In the first case every gamete may copulate with any other and there is sexuality but no sex-differentiation. In the second case only + and — gametes can copulate and sex-differentiation obtains, the foundation for further dif-

ferentiation into egg and sperm not now externally visible. Further development may proceed along different paths. Differentiation may arise between individuals, + and — gametes being then localized in separate members, and the gametes of these same plants may be mutually incapable of union so that only gametes of different plants can copulate. These are here + and — individuals, but the gametes may give no external evidence of a difference. This is the case in Dasycladus according to Berthold and in Ulothrix according to Dodel. Or there may arise differences between the gametes, the one becoming, by the surrender of motility and the assumption of nutritive functions, an egg cell; the other, remaining small and retaining motility, becoming a spermatozoon. Thus hidden differences between + and — germ-cells become conspicuous and there appear "female" gametes and "male" gametes. When the specialized gametes are combined in the same plant it becomes hermaphrodite or monoecious; when separted, dioecious forms appear.

Correns lays emphasis on several points: (1) That the differentiation of gametes into egg and sperm has nothing to do with the union of the two germ-cells for the production of a new individual; or, in other words, that the externally visible differences between egg and sperm need have no connection with the process of fertilization; (2) individuals may be differentiated into males and females without an evident external mark of differentiation either in the individuals themselves or in their germ-cells. The various differential characters of eggs and sperm-cells and all other visible differences between male and female individuals reveal only their different nature, but do not touch the essence of sex itself. Interesting confirmatory observations in this connection are those of Blakeslee on Mucorineæ.

Originally there is present only the "determination" in the germ-cells which renders possible the union of some pairs of germ-cells and prevents the union of other pairs. All else is of a secondary character. With few exceptions the higher animals are unisexual. Among the higher plants many different sexual types occur. Neglecting transition conditions, the main types are hermaphrodite forms where stamens and pistils are united in the same flower; bisexual or monoecious forms, where pistils and stamens are separated into female and male flowers; unisexual or dioecious forms, where the male and female flowers

are borne by different individuals. By far the larger majority of flowering plants have hermaphrodite flowers. Separation of sexual organs on different flowers or different individuals appears here and there as characteristic of entire families, and relatively often as a specific character, or sometimes only as a variation; and this in the most distantly related groups.

Correns entertains no doubt that hermaphroditism is the primary type and dioeciousness the derived. He does not regard as conclusive the arguments advanced by Coulter and Chamberlain that it is impossible to decide which is the primary condition since dioeciousness appears in both the quite low and the higher groups of flowering plants, being related in the former to wind-pollination and in the latter connected with insect-pollination. He observes that sex-separation appears also in other groups without any relation to the high or low degree of other characters. The dioecious condition arises in consequence of the physiological or morphological disappearance of one or the other set of members of the hermaphrodite condition. The "degeneration" of a sexual organ here is really nothing else than an arrest at a certain stage in the development of one or the other element in the hermaphrodite flower (Hofmeister; Goebel), thus producing the monoecious or dioecious conditions. Such change naturally does not proceed without an alteration of the idioplasm of the species involved; the "anlagen complex" of one element must become more or less incapable of development, or latent. As far as we know this process follows independently in both sexes and, in each, internal and external alterations stand in intimate correlation. Male and female flowers of monoecious species are of like high development. The female is not a male arrested at a lower stage of development. The great differences in size and vitality between germ-cells must be regarded as adaptations.

The main points involved in the problem of this investigation concern the *method by which* sex is determined and the *time when* such determination takes place. Since the embryonic and the adult sex-organs contain the anlagen for the characters of both sexes, sex-determination has to do with the question as to which anlage, male or female, shall develop. These conditions demand that the germ-cells have a fixed sex-tendency already before their union at fertilization. Correns emphasizes also that one must not here think of a separation and distribution of

anlagen for the sex-characters into separate germ-cells in the sense that into one animal wander testes-anlagen (determinants of Weismann) and into another ovary-anlagen. This as far as we know is not the case. Both germ-cells carry both sets of sex-characters, as experiments with hybrids abundantly show. That a germ-cell has male or female sex-tendency means only that the male or female anlagen are in condition of capability to develop. As to how one anlage in the germ-cells becomes active and the other is brought to a latent condition we have no positive knowledge.

One may entertain several possibilities respecting the time that sex is determined. He may take the position that the germ-cells have held from the beginning the tendency to develop into one or the other sex—which sex becomes apparent when caused to develop by artificial parthenogenesis—and that the tendency remains unchanged by fertilization; in other words, that the germ-cells are unalterably fixed as to their sex-tendency and thus independently determine the sex of their offspring pure: "progame" determination. Either all the sperm or all the eggs are so determined or only a part of each. Such predestination is commonly ascribed to the egg, and the sperm is thought to be without influence. Accordingly, half the eggs must be male and half female in tendency.

The second position ascribes to the germ-cells before fertilization no fixed tendency to develop into a particular sex, and holds that only at fertilization is the decision made as to what sex the offspring shall have: pure "syngame" determination.

According to the third position the product of the union of the two germ-cells has no fixed sex-tendency. External influences determine only during the later stages of development what the sex of the offspring shall be: pure "epigame" determination. Theoretically an "epigame" alteration of sex must be possible, since the embryo contains both sex-anlagen. All critical investigations, however, both zoological (O. Schultz) and botanical (E. Strasburger), indicate that the means thus far employed in attempting to produce an alteration of sex-tendency have yielded no significant results respecting the actual separation of sex-organs among different individuals. Primarily, attempts must be made to determine whether the germ-cells of unisexual forms have an indifferent sex-tendency or whether they have a fixed tendency. If the latter condition prevails, it

is incumbent next to determine what this tendency is. There are several possibilities: (1) The germ-cells may have the sex-tendency of the plant from which they came, the egg-cells the female, the sperm-cells the male; (2) they may have the opposite sex-tendency; or (3) some of the eggs may be of one sex-tendency and a part of the other, and likewise the sperm. A further problem arises as to how far fertilization plays a rôle in sex-determination, since thus germ-cells of different sex-tendencies may unite; and also how far external influences have significance in that they can act upon the sex-tendency of the germ-cells before fertilization, or at the time of fertilization upon the united product, or after fertilization on the embryo.

Whether a given germ-cell contains a fixed sex-tendency can best be ascertained when such a cell can be caused to develop without fertilization into a sexually mature individual. Such conditions obtain in cases of ''habitual parthenogenesis.'' The facts here at first sight seem to compel acceptance of the position that the sperm-cells play no rôle. However, on closer scrutiny of the facts, doubts are raised as to the validity of such an interpretation. One must not forget that generally eggs that develop parthenogenetically do not undergo a reduction division. Correns states that whatever significance one may attach to reduction, he can not regard such eggs as of like nature with those that have suffered maturation. In the case of ''habitual parthenogenesis'' one deals with phenomena of adaptation. Such adaptation may enable an egg to develop without fertilization even though this capacity depends only on the suspension of a check, which otherwise, through the intervention of a male germ-cell, could exert its influence. In similar manner the sex-tendency also may be influenced. Natural and artificial parthenogenesis yield an indication of the sex-tendency only of the egg. ''Ephebogenetic'' development of sperm-cells, theoretically possible, but practically thus far beset with insuperable difficulties, is urgently required. Merogony furnishes no positive results until we know definitely the rôle of cytoplasm, as distinct from karyoplasm, in heredity.

Correns turns into other fields which seem to lead farther than experiments with artificial parthenogenesis, namely, hybridization. The controlling idea of Correns's investigation is the following: The egg-cells of a diœcious form whose sex-tendency

we desire to ascertain, is commonly fertilized by a sperm-cell of the same species. The sex-tendency of both gametes is unknown. On the other hand, the sex of the offspring resulting from the union of the gametes becomes obvious. In other words by the interaction (in union) of two unknown quantities, X and Y, *i. e.*, the sex-tendencies of the two gametes, there results an organism of known sex; or $x + y =$ sex of organism. Could the value of either x or y be ascertained the equation could be solved and the value of the other unknown quantity determined. These values Correns obtains in the case of the germ-cells of two favorable, nearly related, species of plants one of which is hermaphrodite and the other diœcious. The above figure is not quite accurate, as Correns point out, since a solution of the equation is possible only when the unknown sex-tendency of the germ-cell of diœcious type, as over against the known sex-tendency of the hermaphrodite germ-cell, is so strong as to wholly or almost entirely prevent the development of the latter or to greatly suppress it. The conditions are fully met in those cases where the sperm-cell of a white-flowering pea by fertilization makes possible the development of the egg-cell of a red-flowering pea, so that a red-flowering plant results without showing a trace of the white factor of the sperm. Thus is obtained the effect of artificial parthenogenesis, not only on the egg cell but also on the sperm-cell.

The germ-cells of hermaphrodite forms carry the hermaphrodite sex-tendency and give rise only to hermaphrodite forms. Correns does not regard a hermaphrodite individual as a "mosaic" derived from the union of a germ-cell of male tendency with one of female tendency. However, they must contain the anlagen of such a mosaic. Hermaphrodite germ-cells contain only the hermaphrodite sex-tendency both in the egg-cells and in the sperm-cells. Likewise for monœcious forms, where on the same individual two kinds of sexual flowers appear, male and female, the same position must be taken; *i. e.*, that both kinds of germ-cells, eggs and sperm, carry the same tendency, namely, the tendency to develop into monœcious forms. Each germ-cell thus carries over not the sex of the flower from which it came, but that of the entire plant on which the sexual flowers appeared.

There remains no doubt concerning the monœcious tendency of the germ-cells of monœcious plants. Correns cites in further

support of this position the case of *Dimorphotheca pluvialis*, a "trimonœcious" form where flowers of three kinds, male, female and hermaphrodite, occur in the same head. Since we have here two kinds of sperm-cells (pollen), one from the hermaphrodite flower and one from the male flower, and also two kinds of eggs, embryos can arise in four different ways. If the germ-cells had different sex-tendencies after they are built into a male, a hermaphrodite, or a female flower, four kinds of offspring would arise. All the seed, however, produce the same kind of offspring, *i. e.*, trimonœcious forms. Therefore all the germ-cells of Dimorphotheca must bear the tendency again to give origin to trimonœcious plants. It may be said then, that all germ-cells of a hermaphrodite plant have the tendency again to develop into hermaphrodite plants, whether they be found in stamens or pistils. All germ-cells of monœcious forms have the tendency again to produce monœcious forms whether they arise in male or female flowers. We know, then, the tendency of the germ-cells in hermaphrodite and monœcious types and we can employ these known quantities to ascertain by cross-breeding the unknown tendency of the germ-cells of unisexual plants.

In the first three experiments Dr. Correns employed two species of Bryonia, a genus of the Cucurbitaceæ, growing wild in central Europe. *Bryonia alba* bears a black fruit and is monœcious. *Bryonia dioica* bears a red fruit and is diœcious. In the first experiment (A) he pollinated the pistils (egg-cells) of *Bryonia dioica* with the pollen of *Bryonia alba*. He obtained eleven hybrid offspring from the seed, all female plants and perfectly sterile. These results disclose the following facts: (1) That monœciousness was here recessive to the diœcious conditions; (2) that the egg-cells of *B. dioica* had before fertilization, "progame," a fixed sex-tendency, and all of the same kind. Were this not the case, not all the offspring could have attained the same sex. Had both anlagen, those of the male and those of the female sex, been equally active in the eggs and had a decision as to the definitive sex depended upon a struggle between the anlagen (or upon external influences), the hybrid offspring would have been of dissimilar sexes; (3) the egg-cell has the tendency to develop into a female plant; also the tendency to give origin to such plants as those from which it arose; the physiological sex-determination and the developmental tendency are both female.

The second experiment (B) consisted in fertilizing the egg-cells of *Bryonia dioica* (using flowers from the same plant as used in Experiment A) with pollen from the same species. Of 67 seedlings in the first year 41 came to flower, 21 being male and 20 female, all pure *B. dioica.* Combining the results of this experiment with those of experiment A it becomes positive that the egg-cell possessed a definite sex-tendency, and that the sex was not, however, unalterably determined in it; otherwise in experiment B all the offspring would have become female as in experiment A. The sperm-cells also must have played a rôle in the sex-determination, since until the time of impregnation of the eggs by the male gametes the conditions of both experiments were the same. As far as this experiment discloses, all the pollen-grains might have carried the male tendency. After union with the egg-cells of female sex-tendency a struggle may be conceived to have proceeded, the victory coming now to the female tendency, and now to the male, so that the final outcome resulted in 50 per cent. individuals with definite male characters and 50 per cent individuals with female characters. That this was not the case, the third experiment (C) makes clear.

In experiment C, female flowers of *Bryonia alba* were pollinated by male flowers of *B. dioica.* In other words, *B. alba* furnished the egg-cells and *B. dioica* the sperm-cells. The fruit of the cross was black, and of 87 seedlings, 76 came to bloom the first year, 38 of which were female and 38 male. All the plants showed hybrid characters and were completely sterile. The decision in regard to the sex of the hybrid must have been brought about through the influence of the male gamete (pollen) as in experiment B, since *B. alba* self-pollinated gives rise only to monœcious plants. There is here a second point in evidence, unconnected with the first, against the unalterable "progame" determination of the egg-cells, and in favor of ascribing definite influence to the sperm-cells and to fertilization. The pollen-grains of *B. dioica* can not all have been alike in regard to sex-tendency, else the offspring would all have been of the same sex, since the egg cells of *B. alba* were all alike in their tendency to give origin to monœcious forms. Again, not all the pollen-grains of *B. dioica* can have had the same sex-tendency, else all hybrids, due to the dominance of diœciousness, would have had the same sex. Nor can they have been endowed merely with the tendency of diœciousness, but without a tendency for a

particular sex. Nor can the sex of the hybrid have been determined by the union alone, else in experiment B, where these male gametes united with female gametes all with fixed sex-tendency (the female tendency as determined in experiment A), all offspring would have been alike female plants. Thus there remains only this interpretation: That half of the pollen-grains of *B. dioica* were endowed with the male tendency and half with the female tendency. Since half of the offspring were male and half female, and all of the eggs were of the same sex-tendency, there can not have occurred a struggle for supremacy between the anlagen of the two tendencies (such a condition would yield 75 per cent. female plants and 25 per cent. male plants) but the male sex-tendency must have dominated completely over the female tendency. Sex-determination is thus "progame" and "syngame" alike, but the decision comes "syngame."

Experiments were repeated with *B. dioica* from widely separated regions. Different plants of *B. alba* were also employed. Dr. Correns has had under observation about 1,000 of these hybrids. In 27 experiments, using 16 female plants of *B. dioica* from various regions and 4 plants of *B. alba*, 589 plants were raised and all were females. In 17 experiments, using 5 plants of *B. alba* from different regions and 10 plants of *B. dioica*, 358 hybrids appeared, 171 pure males and 187 pure females. In the body of his paper Correns discusses numerous possible objections and criticisms that might be made in respect to his experiments and the interpretation he gives to his results. All such objections and criticisms are met with very keen and reasonable explanations.

Correns made a fourth series of experiments (D) in which he used plants from a family of only distant relationship to the Cucurbitaceæ. These were a kind of pink, *Melandrium album*, and a plant from a closely related genus, *Silene viscosa*. The former is a diœcious form and Silene is hermaphrodite. Of the seedlings from this cross, using Melandrium as the female parent and Silene as the male, 27 plants came to bloom. They were all female, though in other respects hybrid in character, and sterile. In another experiment (E) Melandrium was fertilized with pollen from its own species (as in experiment E) and there appeared approximately 50 per cent. male plants and 50 per cent. female. The parallel of experiment C with Bryonia was also attempted between Melandrium and Silene, using the latter

as the female parent (the hermaphrodite flowers were castrated) and Melandrium as the male parent. All the seed from this cross was sterile.

Numerous experiments with phylogenetic transition forms ("polyams") between hermaphrodite and monœcious flowering plants on the one hand and hermaphrodite and diœcious forms on the other, *i. e.*, andromonœcious, trimonœcious and gynomonœcious forms—also with androdiœcious, triœcious and gynodiœcious forms—yielded results less definite, it is true, but nevertheless confirmatory (especially as regards the female tendency of the egg-cells of the female plant) of those obtained from hybridization experiments between the end forms as in Bryonia Melandrium and Silene.

The main results may be summarized under three heads: (1) The germ-cells of female individuals all have the tendency to develop into female plants; one half of the germ-cells of the male individuals have the tendency to develop into male plants and one half into female. (2) The definitive sex-determination occurs at fertilization; the original tendency of the female germ-cells can be altered through the sex-tendency of the male germ-cells. (3) When at fertilization germ-cells of unlike sex-tendency unite, the male tendency dominates over the female.

The experiments seem to indicate that sex is inherited. Strictly speaking, however, one can not say that a plant has "inherited" sex, but only that the germ-cells have inherited sex-tendencies. Only the anlagen of sex are transmitted from generation to generation, not the characters ("Merkmale")—the cloak that they have woven for themselves (Naegeli).

Had the hybrids of Bryonia, and those between *Melandrium album* and *Silene viscosa* not been sterile, they would undoubtedly have split up in such a way that the anlage of diœciousness would have been again separated from that of monœciousness and of hermaphroditism, respectively, and the second generation of these diœcious hybrids would have included pure diœcious, hybrid diœcious and pure monœcious (or hermaphrodite) individuals in the Mendelian proportion of 1:2:1. It remains a question whether the diœcious plants would all have had the sex of the diœcious parent or if both male and female plants would have appeared.

In all cases in which the offspring are divided approximately equal in respect to sex, and where the eggs show no external

differentiating characters, as in the great majority of the diœcious Metazoa and man, there appears nothing to contravene the facts and hypotheses regarding sex-determination as presented in the foregoing description of the experiments with certain of the higher flowering plants. However, such cases as are presented by the aphids and the honey-bee, where all fertilized eggs develop into organisms of like sex, are disconcerting from the view-point of the above facts. Correns proposes that the drone eggs of the honey-bee are incapable of fertilization (develop parthenogenetically). He inclines also to the idea that all the eggs may have the male sex-tendency and that femaleness dominates. But since all fertilized eggs develop into females this necessitates, on the hypothesis that there are two kinds of sperm-cells, the further assumption of selective fertilization. The recent discoveries of Meves, Stevens and Morgan, that during spermatogenesis of the honey-bee, certain aphids and phylloxera, respectively, one half of the spermatozoa degenerate (and these probably are the male-producing kind) now brings these cases into very close harmony with Correns's observations on plants. Thus all fertilized eggs must develop into females. The disturbing question still remains as to just how a parthenogenetic female aphid can produce male offspring.

Again when two kinds of eggs are produced, as by phylloxera, daphnids and rotifers, the larger invariably develop (parthenogenetically) into females and the smaller into males. Correns believes that here a proportion of the eggs may have become altered ("umgestimmt") in sex-tendency and that their size-difference stands in correlation with the difference in size of the female and male individuals. In phylloxera this difference, however, does not seem significant. *Dinophilus apatris* seems to be a real exception to the hypothesis that sex is determined by the spermatozoon. Nevertheless, Correns suggests that a portion of the eggs, in consequence of a subsequent alteration or originally, may have retained the male sex tendency; or selective fertilization may obtain, so that only the larger eggs are fertilized by female producing spermatozoa and the smaller by male producing. However, when caused to develop parthenogenetically large and small females appear, the difference in size of the eggs being related to size differences of the offspring and may have arisen through "prospective" adaptation. This argues

for the influence of the spermatozoa in sex-determination and for selective fertilization.

While the facts regarding the honey-bee and Dinophilus offer serious obstacles for the general application of Correns's principles of sex-determination to plants and animals, he finds on the contrary much similarity between his results and the cytological findings of E. B. Wilson for many of the Hemiptera. Taking Protenor and assuming that the spermatozoon with the seven chromosomes (including the accessory) carries the recessive female tendency, and that the spermatozoon with six chromosomes carries the dominant male tendency, then the correspondence between the results is complete. The assumptions made at first sight seem inconsistent, but they appear more reasonable in the light of Correns's observations on *Satureia hortensis* where the female tendency—which becomes patent by reason of the latency of the anlage of the male tendency (in originally hermaphrodite forms)—dominates over the hermaphrodite tendency in crosses, when ordinarily the anlagen for hermaphroditism are active besides the passive anlagen for the female tendency (in gynomœcious forms).

Correns finds it difficult to believe that the idiochromosomes are the material vehicles of the sex-tendency, since the disappearance of the mate of the accessory chromosome in Protenor seems to show directly that it was no sex-determinant. Both germ-cells contribute both anlagen; the idiochromosomes can, therefore, simply aid the development of one sex-anlage or hinder the other. If we accept the idea that they are also the carriers of the sex-anlagen then the spermatozoon of Protenor with six chromosomes would have no sex-anlage; and ephebogenetically developed it would give rise to an organism without sex. If the anlagen are present outside of the idiochromosomes then the spermatozoon thus developed would give origin to a hermaphrodite form. There probably are not two kinds of eggs. The contrary assumption rests upon another; *i. e.*, selective fertilization. There is no experimental evidence of selective fertilization in the case of Hemiptera. If one accepts Wilson's suggestion that in cases like Nezara (where the idiochromosomes are alike) half of the spermatozoa have an active idiochromosome (aiding the development of the female sex) and half a passive one (permitting the male sex to develop), and that the latter may, in consequence of its passivity become reduced (as in

Lygaeus), or have entirely disappeared (as in Protenor), all the eggs may then carry idiochromosomes of like activity and there is no need for selective fertilization. These cases accordingly seem to lend themselves for interpretation very well to the principles above stated for sex-determination in Bryonia. In Mendelian terminology, females are pure zygotes, *i. e.*, homozygotes; males are hybrids, *i. e.*, heterozygotes. Segregation takes place at maturation and produces by the homozygote organism one kinds of germ cells and by the heterozygote two kinds, *i. e.*, male and female in sex-tendency.

The physiological male or female property of the germ-cells which provides for their union and what relates thereto, must not be confounded with the male and female tendency of the germ-cells, or the disposition to give rise to descendants whose germ-cells are again male or female. Though these principles of sex-determination and inheritance discovered for higher plants may not be capable of universal application, there are several points in which the different methods may agree: (1) That each germ-cell has originally a fixed sex-tendency; (2) that the germ-cells of one sex (either the male or the female) have only one and the same sex-tendency, and those of the other partly the one, and partly the other; and (3) that a primarily fixed differentiation in the developmental vigor of the germ cells with different sex-tendencies that unite at fertilization, brings about a decision favorable to one or the other sex.

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